A CONIFEROUS PETRIFIED FOREST IN PATAGONIA

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SYNOPSIS

The present paper contains the results of a detailed investigation of a large collection of silicified coniferous remains from the remarkable petrified forest of Cerro Cuadrado, Patagonia.

Conclusive evidence of only two species (*Araucaria mirabilis* and *Pararaucaria patagonica*), based on seed cones, has been found. *Araucaria mirabilis* belongs to section *Bunya* of the genus *Araucaria*, and the affinities of *Pararaucaria patagonica* are probably with the Taxodiaceae : both species are extinct. The associated wood, branches, twigs and seedlings probably belonged to one or other of the species described. The age of the forest is uncertain, and is at present placed somewhere between Middle Jurassic and Wealden.

INTRODUCTION

THE existence of petrified coniferous plant remains in regions west of the mouth of the Rio Deseado in the province of Santa Cruz, Patagonia, appears to have been first noted scientifically by Dr. A. Windhausen of the Argentine Geological Survey. In 1919 he discovered silicified cones which were kept as curios in stores and farms in the country south-west of the Gulf of San Jorge ; and in 1923 he found abundant petrified material of conifers *in situ* in the region of the Cerro Alto (or Cerro Chato), near the Estancia Belgrano, in a locality about S. lat. 47° 50′ by W. long. 68° 40′ (Windhausen, 1924 : 203, footnote). His collection of silicified wood and cones was passed on to Professor Gothan of Berlin, who gave a short description of them (Gothan, 1925). Dr. Carlos Spegazzini had also (1924) briefly described silicified twigs and cones, the latter similar to those found by Windhausen, which he had received from various donors : these specimens were from the region of the Cerro Madre y Higa, a small volcanic peak about 30 miles north-east of Windhausen's locality (Spegazzini, 1924). Meantime, during 1923–24, a palaeontological expedition from the Field Museum of Natural History, Chicago, had been collecting fossil mammals in Eastern Patagonia, and Dr. Elmer S. Riggs and others made an additional expedition to the region of the Cerro Madre y Higa, and its neighbouring peak about 10 miles to the west, the Cerro Cuadrado, where they found " a considerable number of fossil trees, some with stumps standing, others lying prone with broken branches and cones scattered about them, revealing a forest of fossil Araucaria or Brazilian Pines preserved on the site where it had grown " (Riggs, 1926 : 544 ; Wieland, 1935 : 6).

These discoveries made it clear that in the region of the volcanic peaks of the Cerro Cuadrado, Cerro Madre y Higa, and Cerro Alto, in a district about 10° south of the modern forest of *Araucaria araucana* (Molina) (= *A. imbricata* Pav.) in Chile and Argentina, and about 26° south of the forests of *Araucaria angustifolia* (Bertol.) (= *A. brasiliana* Rich.) in Southern Brazil, there existed the petrified

remains of an extensive araucarian forest. The large Field Museum collection made by Riggs and his co-workers was later reviewed by Wieland (1929, 1935) ; his vividly-presented memoir, however, was without detailed anatomical studies of critical features. A fuller account of one of the cones in the Field Museum, with special reference to the embryo, was given by Darrow (1936). After this, little further botanical investigation of the petrified forest was undertaken, subsequent accounts by Darrah (1939 : 222), Florin (1940 : 36), Arnold (1947 : 313) and Andrews (1947 : 175) being recapitulations of earlier studies, though Florin's later work (1944 : 513) gave a partly revised interpretation of the structure of one type of cone. A non-botanical account of the petrified forest is presented in the memoir by Wehrfeld (1935) of a journey through Santa Cruz. The geology of the regions between the Rio Deseado and the Rio Chico where the forest is situated has also been recently reviewed by Feruglio (1949 : 118 ; 1951 : 35), with special reference to fossil floras of plant compressions found at other localities in this area.

Important new collections of the conifers of the petrified forest have, however, been made by Dr. Franz Mansfeld in the region of the Cerro Alto whilst searching for fossil vertebrates, and in 1936 the British Museum (Natural History) acquired an extensive collection of some 600 specimens from him, some by presentation and some by purchase. Similar material is also widely distributed in other museum and departmental collections : a demonstration of some of it was given by W. T. Gordon at the Geological Society of London on behalf of Dr. Mansfeld (Gordon, 1936). The collection in the Geology Department of the British Museum is a representative one ; in it are included silicified woods, branches and twigs of various sizes, seedlings, and cones, in varying states of preservation and offering remarkable evidence on the nature of the conifers of the petrified forest. The present account is based mainly on this material, though reference has also been made to specimens in other collections : Professor Gothan has described some of this more recently-collected material from specimens in Berlin and elsewhere (Gothan, 1950) and reference is made to this description when the seedlings are discussed. A more detailed study of these South American petrified conifers, and in particular, of the cones, appears to be desirable, especially in view of recent developments in studies of the taxonomy and morphology of the living Araucariaceae (White, 1947 ; Wilde & Eames, 1948, 1952 ; Buchholz, 1949) and of the fossil Araucariaceae (Kendall, 1948, 1949; Cookson & Duigan, 1951). In addition, the remarkable extension and organization of knowledge of the taxonomy, morphology and distribution of fossil conifers in general provided by the work of Florin (1931, 1940, 1938–45) give a more critical basis for comparative interpretation than was previously available.

LOCALITY AND AGE

The site of the petrified forest is in the neighbourhood of the small volcanic peaks of the Cerro Alto (Chato), Cerro Cuadrado, and Cerro Madre y Higa, to the south of the Rio Deseado in the region between lat. 47°–48° S., long. 68°–69° W. (cf. Gothan, 1925, pl. 10 ; Wieland, 1935 : 6, text-fig. 1). More recent accounts of the area where the silicified plant remains are found have, however, shown that the

extent of the forest is considerably wider than suggested in earlier reports. Feruglio's survey (1949 : 128, map opposite p. 134 ; 1951 : 69, 74) indicates a number of additional localities where cones and branches occur, some 25–30 miles to the north-west of the Cerro Alto : these are, Estancia Los Toldos, Canadon de las Cuevas, and west of Cerro Botellon. According to Feruglio's maps, there are at least two localities in the region south of the Rio Deseado called " Cerro Cuadrado " : one lies between the Cerro Alto and the Cerro Madre y Higa in the area originally indicated for the petrified forest, and another some 70 miles to the south-west near to the Estancia La Guitarra. From the latter locality Feruglio has described a quite separate mixed flora consisting of compressions including some araucarian remains (1951 : 62–65, 69), to which reference will later be made. Feruglio's review of the region of the Cerro Alto where the petrified araucarian remains are found (1949 : 128) does not include the vicinity of the Cerro Cuadrado, after which Wieland named the forest, as one of the fossiliferous localities ; the Cerro Alto appears to be the central locality of the forest, and also to be one which has produced very valuable and representative collections, though no doubt much remains to be discovered in other areas..

It is clear, from the various descriptions, that the forest was overwhelmed in an outburst of volcanic activity, the plant remains being embedded in a rhyolitic volcanic ash. Some are found lying weathered out on the surface, showing varying degrees of erosion of surface features, and some of the tree stumps are still standing as noted, for example, by Riggs (1926 : 544), and illustrated by Frenguelli (1941, pl. 25, fig. 1) ; Frenguelli's photograph shows widely scattered trunks, and not a close-set forest formation. Numerous seedling stems, to which reference will later be made, also tend to confirm the impression that the forest was preserved *in situ*, and was overwhelmed whilst regeneration was in progress.

The exact geological age of the forest is still doubtful. Dr. Mansfeld suggested that the rocks from which his specimens were collected were not older than Cretaceous, and that they might even be of Tertiary age ; these estimates appear to have been based on the comparatively modern appearance of the plant structures, rather than on geological data (Gordon, 1936). The horizon has been placed, in other accounts of the petrified forest, as widely apart as mid-Triassic (Windhausen, 1924 : 203 ; 1931 : 201 ; Gothan, 1925 : 197 ; Wieland, 1929 : 60 ; 1935 : 8), Cretaceous (Florin, 1940 : 36 ; 1944 : 513) and Eocene (Frenguelli, 1933, cf. Darrow, 1936 : 328, and Fossa-Mancini, 1941 : 68). Dr. A. F. Leanza, of the University Museum of La Plata, Argentina, very kindly informed me (*in litt.*, 19th June, 1948) that geologically it could then only be indicated that the forest belonged to some stage in the Mesozoic. Windhausen dated the forest as Triassic in the belief that the volcanic ashes which enclose the plant remains form part of an eruptive which, in the geological correlations then in vogue, was comparable in age with the eruptive cycle which in the province of Mendoza originated the porphyritic series found beneath sediments containing a *Thinnfeldia* flora ; eruptive cycles are, however, now known also to have occurred in Patagonia at later stages in the Mesozoic. Feruglio has reviewed again, in some recent publications (1949 : 118 ; 1951 : 35) to which Mr. W. N. Edwards very kindly drew my attention, the problem of the geologic

age of the forest.   He describes a series of floras of plant remains in the form of compressions from a number of outcrops of the complex of volcanic sediments (the " porphyritic series of Bahia Laura ") in the region between the Rio Deseado and the Rio Chico ; and compares them in detail with floras of mid-Jurassic to Wealden age, with special reference to species of *Hausmannia, Cladophlebis, Nilssonia,* and *Ptilophyllum.*   He concludes that the age of the volcanic series is in large part between mid-Jurassic and Wealden ; and that the age of the petrified forest around the Cerro Alto, which occurs in the same complex (although its exact stratigraphic position in relation to the other floras has not been determined), must lie somewhere within the same range (1949 : 131 ; 1951 : 74).   Feruglio also points out that a major unconformity separates this volcanic series from the Upper Cretaceous ; and also that the original determination of a species of *Estheria* from this series in this area as being of Rhaetic age is not now generally accepted.   These latter points further support his delimitation of the age on the basis of the floras.

PRESERVATION AND TECHNIQUE

The plant remains are silicified : the replacement of the organic matter has been fairly complete, and the specimens have not been effectively sectioned by any adaptation of the cellulose peel technique.   Thin petrological slices have accordingly been used (prepared by Mr. J. Fowler of Sheffield) where details of the tissues are required.   However, in some specimens or parts of specimens the silicification has gone so far that little detail can be distinguished : in others the wall structure is well defined, and such details as the nature of pitting in the xylem, and the structure of the embryos in some of the cones, may be observed.   The cut and polished faces of the cones may be used quite effectively for general morphology in many cases ; Wieland relied very largely on this means of examination in his description of the types (Wieland, 1935), which was accordingly lacking in histological details that have proved to be of considerable importance to the interpretation of the general morphology and taxonomy.   Cut and polished specimens form very pretty curios, as the preservation is in rather light silica enhanced by a variety of chalcedonic shades of colour.   Darrow (1936 : 330) has already commented on the tendency for the various tissues of the seeds to be preserved in distinctive shades of quartz.

(1) FOLIATED AND DEFOLIATED TWIGS AND BRANCHES

Araucarites sanctaecrucis n. sp.

(Pl. 1, figs. 4–6, 8–13)

1924. *Araucarites ?* Spegazzini, p. 133, text-fig. 4 (8).
1935. *Proaraucaria mirabilis* (Speg.) : Wieland, p. 27, pl. 13, fig. 1.

DIAGNOSIS.   Woody branches of araucarian habit, radially symmetrical, 5–25 mm. in diameter, occasionally with lateral axillary branches in one row or two opposite rows.   Evergreen : leaves or leaf-scars arranged in a spiral with angle of divergence 3/8 or 5/13, the latter on the thicker branches.   Leaves imbricate and more or less appressed.   Leaf rhomboidal, 8–14 mm. in length, 4–8 mm. in width at its

broadest region, tapering distally to a subacute, somewhat incurved apex, the margins converging at the apex at an angle of 60°–80°. Abaxial surface sometimes showing parallel longitudinal ridges and grooves. Free part of leaf flat, about half the length of the entire leaf, and seated on a flat leaf-base cushion, from which on older branches it has been shed. Leaf-base cushions on older branches 20–30 mm. wide, 5–10 mm. high, with marked longitudinal fissures. Venation of leaves and structure of epidermis not known. Secondary xylem, seldom preserved, with uniseriate and contiguous bordered pits on radial walls of tracheids.

LECTOTYPE. The specimen figured by Spegazzini, 1924, fig. 4 (8).

HYPOTYPE. V. 30941. Geol. Dept., B.M. (N.H.). The specimen illustrated in this paper (Pl. 1, figs. 8, 10, 11).

LOCALITY AND HORIZON. Cerro Alto, Santa Cruz, Patagonia: Between mid-Jurassic and Wealden.

DESCRIPTION.—Many of the detached branches show one side of the specimen much weathered, with surface features nearly obliterated, and the other with excellent preservation of external morphology (Pl. 1, figs. 8, 10, 11). No doubt the better preserved surface was that which lay downwards on the forest floor, whilst the upper surface was subject to processes of weathering as the surrounding rhyolitic volcanic ash was worn away; some specimens of leafy branches are still embedded in the ash (Pl. 1, fig. 1 at L), but most are detached. Pl. 1, figs. 4, 9, 10, 11 and 13 illustrate the habit of branches of varying age. Pl. 1, fig. 11 shows an unbranched stem probably four years old, while figs. 4 and 9 represent thinner branches, probably penultimate branches of the shoot, and show axillary branches similar to that (? 1 year old) in fig. 13, which tend to be arranged in two opposite rows or one row on the parent branch. This condition is found in the penultimate branch systems of many conifers where dorsiventrality in respect of the ultimate branching is common. The defoliated branch of lower order (Pl. 1, fig. 6) may represent the broken apical region of a terminal main branch, with 3 laterals in an apparent whorl.

In the foliated shoots the leaves are arranged in spiral phyllotaxy with angle of divergence 3/8 or 5/13, the latter on the thicker branches: Church (1904 : 99) has noted such spirals of a higher order on the thicker leafy branches in the Recent *Araucaria excelsa*. Pl. 1, fig. 10, *t*, shows the free lamina of the leaf, and at *b* the leaf-base cushion, from the stem shown in Pl. 1, fig. 11. This specimen demonstrates that these plants were evergreen: in transverse section as seen in the cut surface at the upper end (Pl. 1, fig. 8), it shows poorly preserved secondary xylem with 3–4 rather ill-defined growth rings, probably annual. It also shows in some patches of the poorly preserved secondary wood that the radial pitting of the tracheids is uniseriate and contiguous as illustrated in Pl. 1, figs. 3, 7. The transversely cut face (Pl. 1, fig. 8, *t*) also shows the free part of the leaf in sectional view, demonstrating its flat, unkeeled nature. No veins are preserved in the leaf, so that the broad-based leaf habit cannot be definitely associated with parallel venation: nor can the longitudinal striation which is seen on the abaxial surface of the leaf in some specimens (e.g., Pl. 1, fig. 5) be definitely associated with any anatomical feature such as ribs of sclerenchyma. The furrows in such cases may represent the position of lines of stomata, but it has not been possible to demonstrate these structur-

ally, either from sections or cuticles. The older defoliated branch seen in Pl. 1, fig. 12, probably about 5 years old, shows tangentially-extended leaf-base cushions without any clearly-defined scar of attachment of the free lamina of the leaf : it is doubtful whether the longitudinal fissuring in such specimens is entirely a natural condition following on the stretching of the bark with increase in secondary thickening, but it is a common feature in some living araucarians (cf. *A. araucana*, Seward & Ford, 1906, pl. 23, fig. D).

In none of the specimens figured or described in previous accounts of the forest is there any indication of foliated branches : those referred to by Spegazzini (1924) and by Wieland (1935) as *Araucarites ?* and *Proaraucaria mirabilis* respectively are similar to that figured in Pl. 1, fig. 12 of the present account, which has been interpreted as an older branch where the free lamina of the leaf has been shed. After comparison of the variation in morphology of branches of different age in, for example, the living *Araucaria araucana* (cf. Seward & Ford, 1906, pl. 23, A–G), there would seem to be no reason for regarding these thicker defoliated branches as a separate species in the absence of any further criteria of difference : the structure of the secondary xylem is too infrequently and inadequately preserved to be used as such. Various references to similar branches (Darrow, 1936 : 333, 337—where they are identified with *Proaraucaria mirabilis*,—and Arnold, 1947 : 314) have compared them with the living South American species of *Araucaria*, *A. araucana* and *A. angustifolia*, which comprise the section *Columbea* Endlicher, emend. Wilde & Eames. However, from the locality Meseta de Baquero, about 70 miles to the south-west of the Cerro Alto petrified forest, Feruglio has recently described compressions of leafy branches as a new species of *Araucaria*, *A. grandifolia* (Feruglio, 1951 : 62, pl. 3, fig. 5), and he suggests that these might belong to the cone species *Proaraucaria mirabilis*, from the petrified forest, whose vegetative organs, he says, are not known (1949 : 137). He adduces no botanical reasons for this suggestion of relationship, and it is presumably based on geographical propinquity. Comparison of the habit of *A. grandifolia* with that of the leafy branches here described certainly does not suggest specific identity between the sterile branches from the two localities, for *A. grandifolia* has much larger leaves, long, rather narrow, pointed and lanceolate, and of spreading habit. There are no cuticular studies of this species, and on the evidence of the external morphology alone one might even hesitate to assign the branches to the genus *Araucaria*.

Although the general habit of the foliated shoots from the petrified forest suggests comparison with an araucarian type, they cannot be identified on the basis of their external morphology with any living species of *Araucaria*. It is true that the flat and rather broad laminae of the leaves more closely resemble those of the living species of the sections *Columbea*, *Bunya* and *Intermedia* of the genus *Araucaria* than they do those of section *Eutacta* (cf. Wilde & Eames, 1952 ; White, 1947) ; but the combination of characters represented by their relatively small size and flat, somewhat scale-like habit, broad base and rhomboidal form and appressed and imbricate arrangement cannot be matched in any known living species. Indeed, in the absence of information on leaf venation and epidermal characters there is no sound justification for their inclusion in the genus *Araucaria* ; and the only other existing genus

in which they might conveniently be placed is *Araucarites*. *Araucarites* has been used to define fossil cones or shoots of araucarian habit, for various reasons not identifiable with the genus *Araucaria* itself (Seward, 1919 : 256),—though Seward pointed out (pp. 265–6) that the use of this generic name for sterile shoots is not in accordance with sound principles. More recent detailed studies of " araucarian " sterile shoots (*Brachyphyllum*, *Pagiophyllum* : Kendall, 1948, 1948a, 1949) have demonstrated that fossil genera which may be distinguished from *Araucaria* in cuticular structure may have this habit ; though in the case of *Brachyphyllum mammillare* (Kendall, 1949) it is almost certainly related to cone structure resembling that of *Araucaria*. Where, as in the present material, it is not possible to make cuticular investigations, or any definite assignation to fertile material, it is most convenient meantime to retain the artificial genus *Araucarites* to include these branches, which are certainly of araucarian habit. As will be noted in a later section of this paper, the sterile branches are associated with seed cones of two highly distinctive types, one of araucarian and the other probably of taxodiaceous affinity : and in the case of the latter the foliation of the cone pedicel may be superficially compared with that of the separate leafy shoots, which have not been found in connection with cones. The foliated and defoliated shoots may even include more than one species amongst them, though at present these cannot be differentiated. The name *Araucarites sanctaecrucis* is instituted for these sterile shoots, after the province in which the petrified forest occurs.

(2) WOODS
(Pl. 1, figs. 2, 3, 7.)

These are represented by a large number of unbranched woody stems varying from about 8 cm. to 0·5 cm. in diameter, a few being still partially embedded in the rhyolitic ash (Pl. 1, fig. 1, w). Most of these specimens have a complete thick cylinder of secondary xylem, but no distinctive external features : Pl. 1, fig. 2 shows a stem where part of an outer zone, probably representing remains of bark, may be distinguished (c). The preservation of the tissues, so far as examined, is so poor that extensive cutting does not appear to be warranted : but it has been possible to make a few observations on the wood structure. In the stem shown in transverse section in Pl. 1, fig. 2, there is a narrow pith (p), and endarch primary xylem groups surrounded by a wide zone of secondary xylem (x) with several somewhat indeterminate growth rings, probably 12 in number. In radial longitudinal section the pitting of the radial walls of the tracheids of the secondary xlyem can be observed only in a few isolated patches where the organic matter of the walls has probably not been entirely replaced during silicification : this is illustrated in Pl. 1, figs. 3, 7. The bordered pits are uniseriate and contiguous with slight flattening of outline where they adjoin ; but the structure of the medullary rays has nowhere been observed. In another larger specimen (8·5 cm. in diameter : V 30976), probably from a branch 16 years old as judged by the ill-defined growth rings, similar uniseriate pitting has been observed, but again without preservation of medullary ray structure. This wood type so far as it can be defined is not identical with that reported by Gothan

(1925 : 198, pl. 1, figs. 1, 2) and Wieland (1935 : 16) in other specimens from the same locality.   Gothan's wood, named by him *Dadoxylon* (*Araucarioxylon*) sp., showed radial tracheid walls with uniseriate bordered pits, sometimes distantly separate and rounded, sometimes contiguous, but with the indication of the cross-field pitting too indefinite for satisfactory use.

Uniseriate contiguous pitting of the tracheids such as is illustrated here was a type widely represented in the Mesozoic (cf. Seward, 1919 : 165 ; Kräusel, 1949) by a variety of " genera " of fossil woods e.g., *Mesembrioxylon* and *Brachyoxylon*. It has from time to time been interpreted as one transitional phyletically between the " pinacean " and " araucarian " types as these were formerly more or less rigidly defined (e.g., Hollick & Jeffrey, 1909 : 75) : Wieland regarded the Cerro Cuadrado woods as representing such a transitional type (1935 : 16).   However, it has more recently been demonstrated that this type of xylem pitting cannot be regarded as necessarily indicative of transitional or ancestral Araucariaceae, since it is found within the range of variability in xylem structure in individual plants in modern genera of different families of the Coniferales (e.g., *Pinus* : Bailey, 1933 ; *Sequoia* : Bailey & Faull, 1934 ; Araucariaceae : Pool, 1929).   According to Pool (1929 : 599) it is more common in the stem wood of Araucariaceae than is usually recognized.

Without more details of the wood structure, therefore, and in particular of the medullary rays on which keys for wood identification have laid stress (Gothan, 1905 ; Kräusel, 1919, 1945 ; Phillips, 1941), it is not possible to make any effective comparison or identification of these woods.   As will presently be shown, they are associated with two types of cone, one araucarian and the other probably most nearly related to the Taxodiaceae ; and the wood just described might have belonged to either—it corresponds closely with that described for the cone axis of the latter type. Similar wood structure has also been found, very poorly preserved, in the sterile foliated branches of araucarian habit already described.   But it cannot be identified more specifically than as coniferalean wood.

It may be noted in conclusion that Wehrfeld (1935) referred to abundant remains of araucarian petrified wood in the forest, but he adduced no evidence of structural detail.   His illustrations are of uncut woody trunks and branches, some showing " annual " rings (e.g., p. 120, pl. f),   and some of the trunks were very large, one incomplete specimen being reported as 100 metres in length (p. 125).   If this were confirmed, it would seem that some of the trees of the Cerro Cuadrado petrified forest were perhaps the tallest that ever lived, and certainly the tallest that have been found in a petrified state.   One would like to have precise measurements, not only of length, but of diameter at intervals throughout the length.   As Fossa-Mancini has pointed out (1941 : 75), the theoretical maximum height of about 300 feet propounded by Galileo for a tree (cf. Thompson, 1942 : 28) was no doubt considerably exceeded by such a tree as that mentioned by Wehrfeld : and other reports (Feruglio, 1949 : 129) have also recorded very wide trunk bases in the forest.   Leanza is quoted by Feruglio (1949 : 129, footnote) as reporting the base of a fallen trunk of circumference 10·3 metres (i.e., diameter approx. 3·26 metres).   These accounts of gigantism in the trees of the petrified forest refer to the trunks as araucarian ;

as there is no account of wood structure to corroborate this, the identification has no doubt been made on the evidence of associated cones. The wood structure of branches so far examined structurally, as has been pointed out, is indefinitive in character for purposes of identification ; and as will later be shown, while one of the cone types found in the forest is araucarian, the other is probably most nearly related to the Taxodiaceae, in which family at the present day occur the most striking examples of gigantism in trees, comparable with those of the petrified forest. It is perhaps more likely that these giant petrified trunks belong to this family than to the Araucariaceae, but more information on the details of their wood anatomy is needed.

Wehrfeld also reported finding, more rarely, wood of palms. His description of these mentions woods showing yellowish spots which he interpreted as the remains of the principal vascular bundles ; but no structural evidence was given to support this interpretation, nor has it so far been possible to obtain evidence of the presence of monocotyledons from any other woods examined. The " yellowish spots " which he described may represent variation of the mineral differentiation in the stems rather than the position of vascular bundles ; for the petrifactions in the forest tend to show differentiation of colours in the quartz.
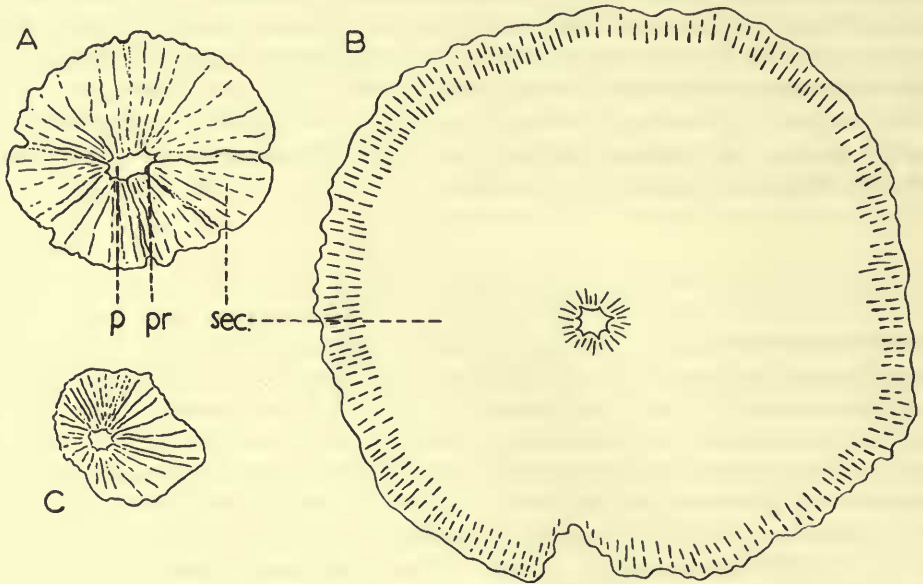
(3) SEEDLINGS

(Pl. 2, figs. 14–25 ; Text-fig. 1, A–C.)

There are numerous (about a couple of hundred) petrified structures, many of them looking like small corms or carrots, which vary in shape from ellipsoidal to turbinate (Pl. 2, figs. 14, 15, 17,), with intermediate forms such as that shown in Pl. 2, fig. 16. Most of these specimens are detached : but Pl. 2, fig. 14 shows one (s) lying prone and partially embedded in the matrix. The turbinate forms vary in size from 4 cm. in height and 5 cm. in widest diameter to 1·5 cm. in height and 2·2 cm. in diameter ; the ellipsoidal or clavate forms are more uniform in size, averaging 4·5 cm. in height and 1·5 cm. in widest diameter. None of these structures shows any continuation at either end of the axis into a leafy shoot or a well-defined root : Pl. 2, figs. 18 and 19 show one specimen with a prolongation of the broader end of the axis which bears no evidence of insertion of lateral organs.

From external examination of the specimens and from examination of cut and polished surfaces it may be seen that most are partially or completely decorticated (Pl. 2, figs. 15, 17), and that a few have what appears to be a fairly thick periderm (Pl. 2, figs. 18–20, 22, *pd.*). The core of such specimens is composed of a thick zone of poorly preserved tissue resembling secondary wood (Pl. 2, figs. 19, 20, 22, *x*) and a narrow region in the centre probably comprising pith and primary xylem. The decorticated specimens show on their external surfaces longitudinal fissures and markings (Pl. 2, figs. 15–17), some of which might indicate the position of primary medullary rays in the xylem ; however, as such markings may also be found on corticated specimens (Pl. 2, fig. 18), they may be due, at least in part, to cracking during decay and preservation.

Some thin sections have been prepared from the more promising of these specimens with a view to studying the arrangement and detailed structure of the tissues for

comparison with the gross morphology.   The preservation is unfortunately very
poor in most of the specimens cut : but Pl. 2, figs. 23–25 shows the centres of trans-
verse sections taken at the top (broader) end, middle, and base (narrower end) of a
specimen similar to that shown in Pl. 2, fig. 15, where preservation was better than
in most.   The outlines of the whole sections are shown in Text-fig. 1, A–C (correspon-
ding with Pl. 2, figs. 23–25), where it can be seen that there is a medullated stele
with the pith region (*p*) widening from the base upwards, whilst it also changes from
rounded to ovate in shape in transverse section.   Pl. 2, fig. 21 shows this pith in
median longitudinal section of the broader end of the specimen ; the innermost

TEXT-FIG. 1.   Seedling (cf. *Araucaria mirabilis*).   Transverse sections through a seed-
   ling at top, middle and base of swelling (cf. Pl. 2, fig. 15), showing pith (*p*) in centre
   surrounded by primary xylem groups (*pr*) and secondary xylem (*sec.*).   (cf. Pl. 2, figs.
   23–25).   V. 30951.   × 5.

elements of the xylem ring are narrower than those forming the bulk of the xylem,
and the pith is notable for its more or less isodiametric, thick-walled cells.   The
bulk of this specimen is composed of poorly preserved tissue resembling secondary
xylem traversed by medullary rays, in which structure of pits cannot be distinguished.
The primary xylem groups which abut on the pith increase in number from below
upwards, and the condition appears to be endarch, with stem structure throughout,
and with no evidence of traces passing out to lateral appendages.   Other sections
from specimens similar to those in Pl. 2, figs. 16, 17 show the same general arrange-
ment of the tissues (cf. Pl. 2, fig. 22) ; the structure of the tissue resembling secondary
xylem can only be distinguished in a few better-preserved patches in some of the

longitudinal sections, where coniferalean pitting, of the type illustrated in Pl. 1, figs. 3 and 7, may be distinguished on the radial walls.

These curious bodies must therefore be interpreted as swollen intercalary organs, having stem structure but without any evidence of lateral appendages, and with marked development of a tissue resembling secondary xylem. Their identification is a matter of some difficulty; but the structures are so numerous, and the intercalary swelling is so striking in all of them, that they must have some regular significance in the vegetation of the forest. Wehrfeld figured a number of such structures (1935 : 129), and referred to them as " a scientific novelty—a series of fossil araucarias," without, however, substantiating in any way the reference to the Araucariaceae. Gothan, too, in a recent brief study (1950), has described such structures as those in Pl. 2, fig. 17—the turbinate or fig-shaped forms—and believes the most likely interpretation to be that they are of the nature of insect galls, terminal on branches, where hypertrophy of the wood of the branch has been caused with the larva living in the centre, and with the gall eventually dropping off the end of the branch. He also believed they might be araucarian, but had found no evidence of any such galls in living Araucariaceae. It has not, however, been possible to find any evidence that the structures are other than intercalary, or that the turbinate forms are different in kind from the ellipsoidal forms; and in some of the specimens sectioned there is a definite pith including thick-walled cells and with no sign of any larval intrusion. There remains, however, the possibility that these might be fungal stem galls of an intercalary nature; such intercalary stem swellings are known in some cases to be caused by fungi, as in the case of *Peridermium* galls on *Pinus* stems; but no records of such galls on araucarian stems have been found, though Connold (1909 : 132, text-fig. 159) has described long, irregular tumours on the roots of *Araucaria imbricata* which do not resemble the present structures at all. In the case of either terminal or intercalary stem galls, however, one would expect to find some evidence of lateral appendages, and there is none. On the other hand the size, shape and internal structure of these bodies all tend to emphasize their similarity to broken first-year seedlings of the genus *Araucaria* in the sections *Bunya* and *Columbea*, where tuberous development in varying degree is found in the hypocotyl, which is of stem structure with early incidence of secondary thickening (Dürr, 1865 : 103; Hemsley, 1901; Seward & Ford, 1906 : 333; Shaw 1909; Hill & de Fraine, 1909 : 212; Hickel, 1911 : 160).

Wieland has figured certain branch-like structures (1935 : 27, pl. 13, fig. 2) as bases of second-year seedling stems of *Proaraucaria*, with broken root bases: but if these are indeed older seedlings, they are not markedly tuberous, and there is no evidence of any relationship with the smaller structures here described. The tuberous habit in seedlings in general is sporadic: it appears to be rare amongst gymnosperms, occurring in the Cycadales in *Encephalartos*, and in the Coniferales in the two sections of the genus *Araucaria* just mentioned. The proximity of these numerous tuberous bodies to fertile cones belonging to the section *Bunya* of the genus *Araucaria*, which will be described in the next section, also tends to corroborate their interpretation as araucarian seedlings: and the fact that the embryos in the seeds of these cones are dicotyledonous might suggest that the markedly ovate form

of the pith at the upper end of the seedlings is related to a stelar adjustment below the level of the insertion of the vascular supply of two cotyledons on opposite sides of the hypocotyl axis.

So far as has been ascertained, this is the only record of petrified seedlings. Kendall (1949, text-fig. 1, J.) has drawn attention to a curious specimen, found as a compression, from the Mid-Jurassic Estuarine Series of Yorkshire which she has interpreted as a seedling stage of *Araucarites phillipsi* Carruthers, but no other such records are known to the writer.

Mr. W. N. Edwards informs me that there is a specimen in the Sedgwick Museum, Cambridge, from the Lower Greensand of Upware, Cambridgeshire, which was figured by Keeping (1883 : 150, pl. 8, fig. 7) as "a small fruit (?) ferruginized," but which superficially at least is very similar to some of the smaller araucarian seedlings from Patagonia.

(4) CONES

The cones, which represent the best preserved part of the collection, are of especial interest, since petrifactions of reproductive organs of fossil conifers are seldom found, though petrified coniferous woods are abundant. Two distinct types of seed cone are represented, but no male cones or pollen-producing organs have been found. These two types of cone have already been partially described by Spegazzini (1924), Gothan (1925), and Wieland (1935) ; but detailed studies of the structure, which affect the interpretation of the morphology and consequent assessment of the relationships of the cones, have not been made, with the exception of Darrow's investigation (1936) of the structure of the embryo of *Araucaria mirabilis*.

Araucaria mirabilis (Spegazzini)

(Pls. 3, 4, 5 ; Text-figs. 2–4)

1924. *Araucarites mirabilis* Spegazzini, p. 126, text-figs. 1–3, 4 (1–7).
1925. *Araucaria windhauseni* Gothan, p. 200, pls. 2–7, pl. 8, fig. 1.
1929. *Proaraucaria mirabilis* (Speg.) Wieland, p. 60.
1929. *Proaraucaria elongata* Wieland, p. 60.
1931. *Araucaria mirabilis* (Speg.) Windhausen, p. 201.
1935. *Proaraucaria mirabilis* (Speg.) : Wieland, p. 19, pl. 1 ; pl. 7, figs. 2, 3 ; pl. x ; pl. xi, figs. 1, 2, 4 ; text-fig. 4.
1935. *Proaraucaria mirabilis* var. *elongata* Wieland, p. 26, pl. 8, fig. 1 ; pl. 9, fig. 2 ; pl. 12, fig. 4.
1935. *Proaraucaria patagonica* Wieland, p. 26, pl. 6, figs. B, D, E, F.
1935. *Proaraucaria mirabilis* var. *minima* Wieland, p. 26, pl. 6, fig. A ; pl. 12, fig. 3.
1936. *Proaraucaria mirabilis* (Speg.) : Darrow, p. 328, text-figs. 1–13.
1936. *Araucarites mirabilis* Speg. : Gordon, p. 14.
1939. *Proaraucaria mirabilis* (Speg.) : Darrah, p. 222, text-figs. 133, 134.
1940. *Araucaria mirabilis* (Speg.) : Florin, p. 36.
1944. *Araucaria mirabilis* (Speg.) : Florin, p. 513.
1947. *Proaraucaria mirabilis* (Speg.) : Arnold, p. 313, text-fig. 156.
1947. *Proaraucaria mirabilis* (Speg.) : Andrews, p. 177, text-fig. 121.
1948. *Proaraucaria mirabilis* (Speg.) : Wilde & Eames, p. 312.
1949. *Proaraucaria mirabilis* (Speg.) : Feruglio, p. 129.
1951. *Proaraucaria mirabilis* (Speg.) : Feruglio, p. 35.

EMENDED DIAGNOSIS.   Seed cones varying in shape from spherical to somewhat ellipsoid, and in size from about 8 to 4 cm. in height and 8 to 4 cm. in diameter. Cone-scales numerous, arranged in a close spiral, one-seeded, with thick woody wing and deciduous laminar tip, which on dropping reveals the large woody ligule on top of the rhomboidal apophysis of the bract ; the fertile scale is fused with the bract for about two-thirds of its length, so that the depth of the ligular sulcus is about one-third of the length of the fertile scale.   Cone-scales of mature seed cones (delaminated) 13–16 mm. long and 10 mm. wide including the wing, tapering somewhat towards the base.   Ligule 4 mm. wide, 1·2 mm. high, about 5 mm. long.   Seed 8 mm. long and 3 mm. wide and deep, inverted, albuminous, apparently embedded in the fertile scale tissue ; testa with a thick stony layer.   Embryo large, dicotyledonous, with numerous spirally twisted suspensors at base.   Evidence on mode of seed dispersal lacking.

Axis of cone wide, with a wide pith including branched sclereids, surrounded by a narrow ring of separate vascular bundles each with a wide outer sheath of fibrous extra-phloem tissue.   Vascular supply of cone-scale double, the bract trace single and arising separately from the base of the leaf-gap in the axis stele, the fertile scale supply of two strands, arising from either side of leaf gap, which fuse with inversion : both bract and fertile scale supply fork in base of cone-scale to give a lower and an upper (inverted) series respectively, the lower series passing out to the apophysis and laminar tip of the bract accompanied by a series of resin canals, the upper series terminating in the large strongly vascularized ligule.

DESCRIPTION.—The species is represented by a large number of specimens in the collection ; most of these are isolated specimens, but a few are still partially embedded in the matrix (Pl. 3, fig. 26).   Some of the cones must have been mature, as they contain fully formed embryos in the seeds, while others have no embryos, though the cones may be as large as those which do.   The cones vary in size from 8 cm. in length and diameter to 4·4 cm. and 4 cm. in length and diameter respectively, and in shape from nearly spherical to ovoid or ellipsoid.   There is no evidence to suggest that the smaller cones are necessarily immature, for one about 5 cm. in length and diameter (V. 30975) has fully formed embryos in the seeds.   Some specimens appear more markedly elongate, with an ellipsoidal section, than others (e.g., Pl. 4, figs. 38, 42) : such cones were interpreted by Wieland (1935 : 26) as a distinct variety, *Proaraucaria mirabilis* var. *elongata*, but structurally it has not been possible to differentiate these types, and there is evidence from the cone figured here that the condition has been exaggerated by considerable crushing prior to petrifaction, as may be seen in the compressed and broken outer parts of the scales in Pl. 4, figs. 40, 42, while the proximal part of the scales has withstood the compression, being reinforced, perhaps, by the woody tissues of the testa.   The cones have been petrified before the shedding of the seeds in most cases ; no separate petrified seeds nor cone-scales have been found, but there are a few specimens, such as those figured by Wieland (1935, pl. 6, E) and interpreted by him as another species, *Proaraucaria patagonica*, which no doubt represent the naked axes of the cones after the cone-scales have been shed (e.g., V. 30969).   They correspond in size with the measurements of the cone axes themselves ; one has been sectioned, and shows a wide pith

with sclereids, and peripheral vascular bundles. The surface features correspond closely with those found in cones of living araucarians after shedding of the cone-scales (cf. Seward & Ford, 1906 : 361), with a reticulum of low ridges outlining rhomboidal areas no doubt representing the areas of attachment of the scale bases to the cone axis. The absence of any separate cone-scales, which Gothan (1950 : 153) has emphasized as a feature suggesting that these cones did not shed their scales at maturity, and as one which might separate them generically from those of other species of *Araucaria*, may well be explained in terms of the season in which the forest was overwhelmed. The seeds in the cone-scales in the final year of growth had not been shed, and the previous year's had germinated and are probably represented in the forest by the very numerous petrified seedlings to which reference has already been made.

Various views of external features of cones are shown in Pl. 3, figs. 26–31, Pl. 4, figs. 38, 39, and Pl. 5, fig. 46. Inserted on the cone axes are a large number of close-set ligulate cone-scales, each of which bears a single large inverted seed sunken in its tissue on the upper surface. The distal, abaxial faces of the cone-scales are seen arranged in a close spiral forming some 55 orthostichies (so far as has been examined). The surface morphology of the cone-scales varies, probably according to the age and condition of the cone and also to some extent to the degree of weathering of the surface, as shown in Pl. 3, figs. 28, 29, 31, 34, Pl. 4, figs. 38, 39, and Pl. 5, fig. 46. Pl. 4, figs. 38, 39, 42 show a cone where in surface view the cone-scales have laminar, longitudinally striated tips (*t*). In earlier descriptions of the cones, Gothan (1925, pl. 2) and Spegazzini (1924, text-figs. 1*b*, 4 (6)) have illustrated some with a similar triangular lamina on the cone-scales, and Wieland mentions this feature (1935 : 175, pl. 10, fig. 2). Most of the cones, however, show surface morphology of cone-scales as illustrated in Pl. 3, figs. 28, 29, and Pl. 5, fig. 46, with prominent apophysis of bract (*a*) with marked lateral wings (*w*), and a large ligule (*l*). Consideration of sections of the specimen in Pl. 4, figs. 38, 42, leaves little doubt that this latter condition is the result of the dropping of a laminar tip, though erosion of surface features may occasionally account for it. Pl. 4, figs. 40, 42, show this laminar tip *t*, covering the ligule *l*, in radial longitudinal section ; and Text-fig. 4, A–I, and Pl. 4, fig. 43, Pl. 5, fig. 54, from a tangential longitudinal series, demonstrate the same relationship between the laminar tip and the ligule. There is, too, some structural evidence of an absciss zone at the base of the laminar tip, e.g., at A in Pl. 4, fig. 40. The lateral wings of the cone-scales are also seen to be present in the series of tangential sections, though they tend to be obscured in surface view (Pl. 4, fig. 39) as compared with the cones with delaminated scales. In any respect other than the presence or absence of a laminar tip it is difficult to separate the two cone types : in both, seeds with fully formed dicotyledonous embryos of the same type have been found. The much smaller cone illustrated in Pl. 3, figs. 31–34, shows similar longitudinally striated laminae clothing the exterior of the cone ; in section (Pl. 3, figs. 32, 33) no ovules can be distinguished, and it may be either a young cone or one with abortive or unpollinated ovules. The comparatively large ligule can again be distinguished behind the distal lamina of the cone-scale (Pl. 3, fig. 33, *l*). There seems little doubt that the three cone types just described represent

different stages in the development of the same cone species ; in many of the living Araucariaceae there is a laminar tip or spine on the cone-scale which often drops off when the cone is ripe (cf. Pilger, 1926 : 255).

The ligulate cone-scales are modified in form towards the base of the cone, where they are sterile.   Pl. 3, fig. 30 shows the transversely cut tip of a cone pedicel (pl), around which are a number of such sterile cone-scales of simplified form, which pass over gradually into the fully formed fertile cone-scales above.   This is a character of araucarian cones which has been emphasized by Seward & Ford (1906 : 354, text-fig. 22A) as contrasting with the condition in the Pinaceae where the cone-scales
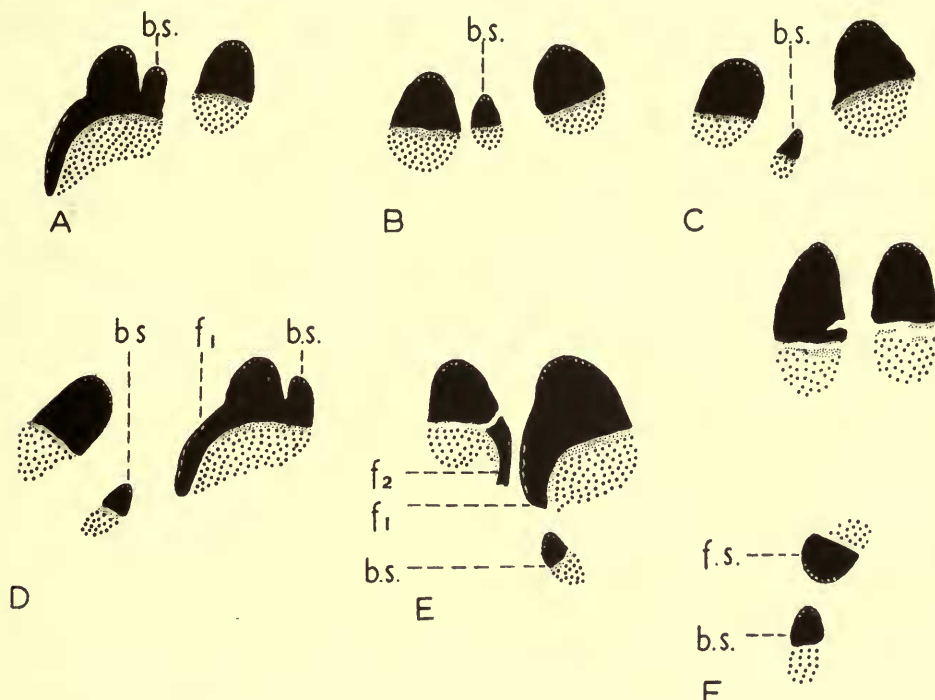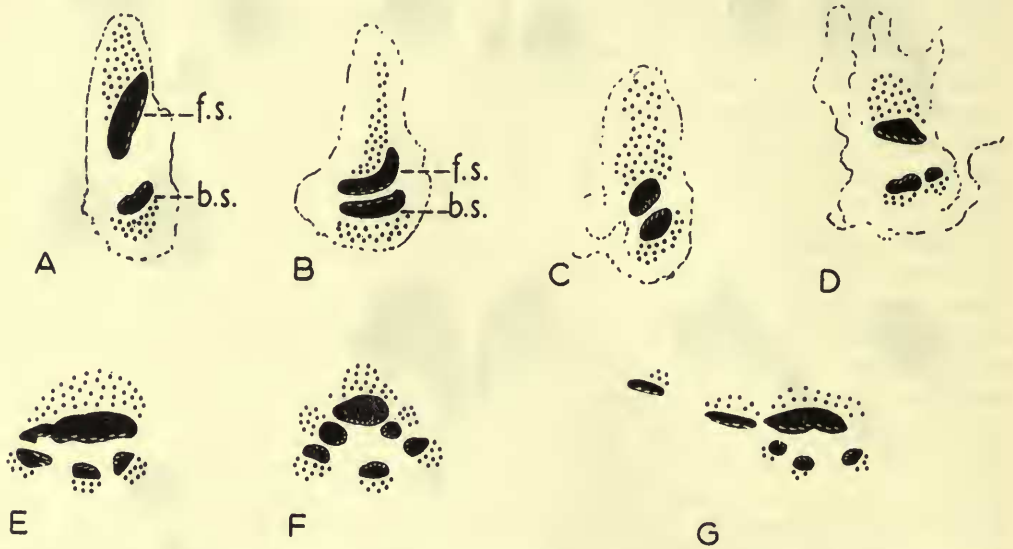

TEXT-FIG. 2.   *Araucaria mirabilis* (Spegazzini).   Transverse sections through vascular bundles of cone axis stele, showing from base upwards a series in the detachment of the bract supply (*b.s.*) and fertile scale supply ($f1$, $f2$) of cone scales.   The two traces of the fertile scale supply fuse with inversion to give a single bundle (*f.s.*).   The pith lies to upper side, cortex to lower side, of the vascular bundles, where xylem is shown black, with protoxylem white, phloem finely stippled, and extra-phloem tissue coarsely stippled.   V. 30958.   × 27·5.

are much more sharply differentiated in form from the foliage leaves, and succeed them more abruptly.   In none of the fossil cones examined is there critical evidence of the foliation of the pedicel, or of attachment to any of the leafy branches which are found amongst the remains of the forest.

The axes of the cones are thick (Pl. 3, fig. 27), with a wide pith and narrow ring of separate vascular bundles, seen at p and v respectively on the transversely frac-

tured surface and in Text-fig. 2 in transverse section. The pith contains branched sclereids; the tissues of the vascular bundles are ill-preserved, but in patches of better preserved tracheids the xylem pitting varies from uniseriate to biseriate and alternating, with the pits separate, and each bundle is endarch, with a narrow zone of phloem, outside which is a deep arc of extra-phloem tissue (? pericycle) as seen in Text-fig. 2, *e.p.* This extra-phloem tissue is much better preserved than is the phloem, and consists of large, thick-walled, sometimes branching cells resembling the sclereids of the pith rather than a typical fibrous tissue. Comparison of this type of cone axis with that of other conifers reveals the striking similarity with that of living araucarian cones. Thomson (1913 : 4) has drawn particular attention to the exceedingly large size of the pith in the cone axis of the Araucariaceae, especially
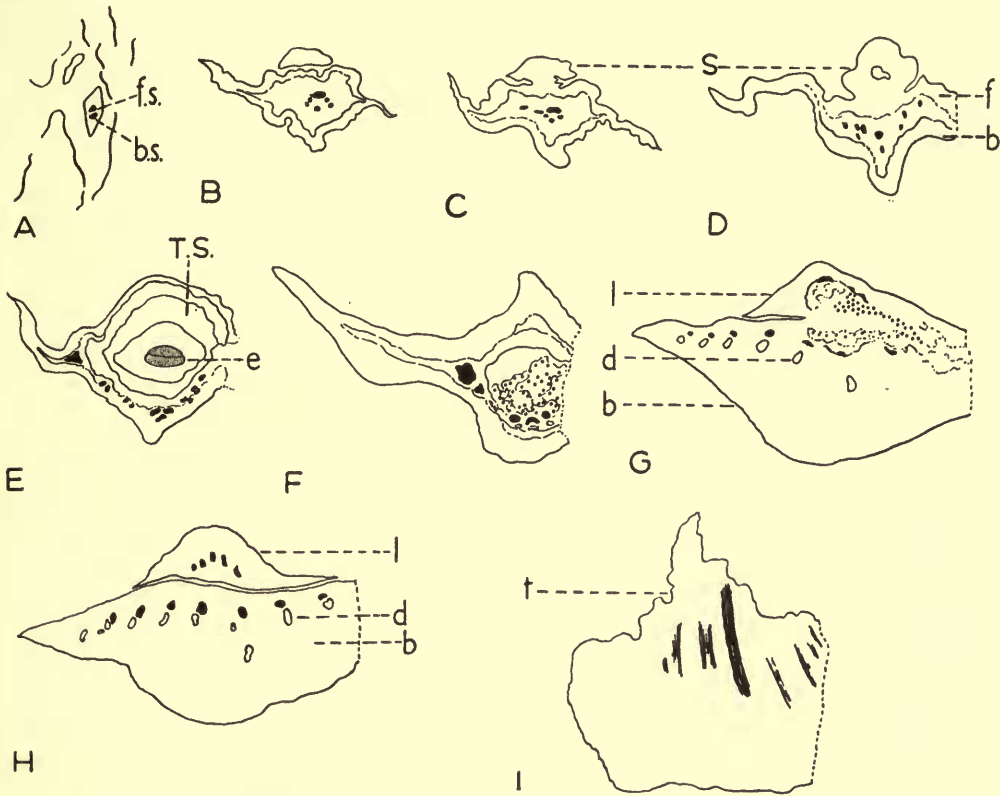

TEXT-FIG. 3. *Araucaria mirabilis* (Spegazzini) (cf. cone in Pl. 4). Tangential longitudinal sections of cone-scales from base outwards, showing splitting of the two bundles *b.s.*, *f.s.*, in base (cf. Text-fig. 2), to give the vascular supply of bract and fertile scale respectively. Xylem shown black, with protoxylem white, extra-phloem tissue coarsely stippled. V. 30957. × 27·5.

in the seed cones, where it may reach 1 in. in diameter. The sclereids of the pith and the extra-phloem or fibrous pericyclic tissue are, too, characters associated with the axis anatomy of the living Araucariaceae (cf. Seward & Ford, 1906 : 337).

   A study of the detachment of the cone-scale vascular supply from the axis stele has been made in transverse sections of the cone axis ; Text-fig. 2, A–F, illustrates successive stages, from below upwards, in the detachment of the traces, as seen in different sectors of the wide cylindrical stele. This has proved more satisfactory than the use of a series of sections, as 1·5–2 mm. may be lost between successive sections in preparing a series, while the spiral succession of the numerous scales is so close-set that from one section a close series of stages can be obtained. The bract supply,

b.s., comes off as a single trace from the base of the leaf-gap, and free from the fertile scale supply, *f.s.*, which is derived from the fusion of two strands, *f1*, *f2*, detached separately from either side of the leaf-gap above the bract supply.   These two strands rotate through 180° while fusing, so that the resultant fertile scale fusion bundle is inverted (Text-fig. 2, D–F).   In the base of the cone-scale there are, therefore, two bundles, the upper one inverted.   Text-fig. 3 shows their subsequent behaviour in tangential sections of the cone illustrated in Pl. 4, fig. 38, taken in series from the inside of the cone outwards : Text-fig. 4, from the same series, shows

TEXT-FIG. 4. *Araucaria mirabilis* (Spegazzini) (cf. cone in Pl. 4, and Text-fig. 3). Tangential longitudinal sections of cone-scales from base outwards, to show vascularization of bract (*b*), its laminar tip (*t*), and fertile scale (*f*) with ligule (*l*). Xylem shown black, sclerotic tissue coarsely stippled.   *S* = seed, *T.S.* = stony layer of testa, *e* = embryo, *d* = resin ducts, *f.s.* = vascular supply of fertile scale, *b.s.* = vascular supply of bract. V. 30957.   × 5.

the relationship of the bundles to the cone-scale morphology throughout the scale and into the laminar tip.   Each of these two bundles in the scale base branches, the bract bundle first (Text-fig. 3, D–E), and this lower series, though incompletely preserved in the region below the seed (Text-fig. 4, E, F), appears to supply the apophysis and the laminar tip of the bract (Text-fig. 4, G, H, I ; cf. Pl. 4, fig. 43 ; Pl. 5, fig.

54).   In the outermost region of the cone-scale (Text-fig. 4, G, H, and Pl. 5, fig. 54) structures resembling resin canals (d) lie below the bundles.   Pl. 4, figs. 43, 45 show obliquely cut bundles (v.b.b.) supplying the laminar tip of the bract ; these bundles are accompanied on either side by a strand of cells with dark contents (d), which may represent the upward extension of the resin canals into the laminar tip.   It has not been possible to demonstrate whether, as in *Araucaria bidwilli*, there is a distinct system of bundles ending blindly in the apophysis, with the laminar supply branching off farther back.

The upper inverted fertile scale bundle branches farther out in the scale base (Text-fig. 3, E–G), and forms a strong inverted upper series, probably supplying the base of the single inverted seed (Text-fig. 4, F) as well as the large ligule (Text-fig. 4, G, H, and Pl. 5, fig. 54).   Pl. 4, fig. 44 demonstrates a vascular strand in the ligule. Pl. 5, fig. 53, taken from a delaminated cone, also demonstrates vascularization of the large ligule (l), along with the distinct series of the bract (b).

There are two notable features here for comparison with the living species of *Araucaria* : the separate origin of the bract and fertile scale supplies, and the strong vascularization of the ligule.   Only in the section *Bunya* Wilde & Eames amongst the living araucarians are these two conditions found (Eames, 1913 : 24 ; Aase, 1915 : 297 ; Wilde & Eames, 1948 : 322 ; 1952 : 44).   This is probably the first time that it has been possible, in a fossil araucarian cone, to demonstrate these characters, which are of critical importance in considering the taxonomy and interrelationships of living araucarians.

Text-fig. 4 and Pl. 5, fig. 54, also serve to demonstrate the lateral winging of the cone-scale ; this " winging," already noted in the external morphology of the cones, extends from near its base out to the apophysis, as seen in Text-fig. 4, B–H.   A similar condition is found in the delaminated cone shown in Pl. 5, figs. 46, 50, 53.   The wing is about as wide as the body of the seed, and is relatively thick ; it is supplied by vascular bundles of the lower (bract) series (Text-fig. 4, G, H, and Pl. 5, fig. 54).   The tissues of the wing have evidently been woody, as may be seen in the cone in Pl. 5, fig. 50, where a core of thick-walled pitted cells is found, possibly of the nature of a transfusion tissue, and in Pl. 5, figs. 53, 54 where there is a deep hypodermal zone of thick-walled cells.   Cone-scales as thick and woody and as widely winged as these must have been are found amongst living araucarians only in the section *Bunya* (Wilde & Eames, 1952 : 44).

The morphology of the ligule, already noted in surface view of the cones, is seen in tangential longitudinal sections in Text-fig. 4, G, H, Pl. 5, figs. 53, 54, and in radial longitudinal section in Pl. 4, fig. 40, Pl. 5, fig. 52.   Its vascular bundles have already been noted ; its ground tissue is similar to that of the wings, and no doubt it was also woody.   The depth of the sulcus between the ligule and the bract may be exaggerated by artificial splitting between the two, extending apparently deep into the scale, the space occupied by clear quartz.   The cone in which the split is most clearly and perhaps most naturally seen is illustrated in Pl. 3, figs. 35–37 : it will be noted that, where the scale is not quite medianly cut as at A in the radial longitudinal section of the cone in Pl. 3, figs. 35, 36, the split extends deeper than the level of the base of the seed, but where a more median cut of the seed is found, as at B, the split stops

towards the base of the seed. This is also demonstrated in the tangential longitudinal series of another cone in Text-fig. 3, F–H, where in Text-fig. 3, G, just outside the base of the seed, the ligule has separated from the bract on the margin but not yet in the median plane. It will be seen from Pl. 3, figs. 35, 42 that the ligular sulcus is about one-third the depth of the fertile scale, the fertile scale being fused with the bract for about two-thirds of its length; and this is about the same proportion for the depth of the ligular sulcus as in the living *Araucaria bidwilli* in mature cones (cf. Wilde & Eames, 1948: 325; Pilger, 1926: 256, text-fig. 139, A). Wieland based his generic definition of these cones as *Proaraucaria* on the greater depth and size of the split separating ligule from bract, as well as on the larger size of the ligule, in comparison with the condition in living species of the genus *Araucaria* (Wieland, 1935: 19), and he regarded the fossil species as representing an intermediate stage in the evolution of the cone-scale, with less complete fusion of bract and fertile scale. His figures, however, nowhere make clear the natural depth of the split separating ligule from bract. From the present examination there is no evidence to show that the difference in degree of size of ligule and depth of sulcus separating it from the bract in the fossil and in living species is such as to warrant the erection of a new genus; the fossil is closely similar to *Araucaria bidwilli* in these respects.

The relationship of the seed to the upper surface of the scale is shown in Text-fig. 4, B–G, Pl. 4, figs. 40–42, and Pl. 5, figs 47, 50–52. The single large inverted seed (S) appears as if embedded in the scale tissue; this is probably best seen in the tangential sections in Pl. 5, figs. 47, 50, the conspicuous stony layer of the testa (T.S.) lying within an outer sheet of tissue (F) which is continuous with the surface tissue of the wing of the scale on either side of the seed. Within the stony layer the nucellus is imperfectly preserved, but in many seeds the embryo sac may be defined, enclosing the endosperm with an embryo embedded in it (Pl. 5, figs. 47, 50–52, *en* and E). The dicotyledonous embryo is seen entire in Pl. 4, fig. 41, where the polished radially cut surface of the cone is photographed; and embryos are seen cut in transverse section of the cone at E in Pl. 5, figs. 48, 51, and Text-fig. 4, E, in tangential longitudinal sections of the cone in Pl. 5, figs. 47, 49, 50, and in radial longitudinal sections in Pl. 4, figs. 40–42 and Pl. 5, fig. 52. Plate 4, fig. 41 and Pl. 5, figs 48 49 demonstrate the two cotyledons (*co*), and Pl. 4, figs. 41, 42, show the orientation of the embryo with the thick radicle pointing towards the micropylar end of the embryo sac, where there is a tangled mass of suspensors (*ss*) (Pl. 5, fig. 51). The embryo need not be described in detail as this has been done by Darrow (1936); but dicotyledonous embryos of similar type have been found in both the laminated and delaminated types of cone (cf. Pl. 4, fig. 42, Pl. 5, figs. 47–51), and the orientation of the plane in which the median lines of the two cotyledons lie varies from one more or less parallel to the surface of the fertile scale (Pl. 5, figs. 47, 49) to one at right angles to it (Text-fig. 4, E).

RELATIONSHIPS. From the fuller account of these araucarian cones which it has now been possible to give and with particular reference to the critical characters of mode of origin of the vascular supply of the cone-scale from the axial stele, size and nature of wing of cone-scale and size and nature of ligule, two major conclusions emerge which contrast with many of the previously expressed views on the

relationships of this species. The first is that there are no grounds for its taxonomic separation into a new genus *Proaraucaria*, which was effected by Wieland (1935) because he believed the cleavage between ligule and bract to be deeper than in any living species of *Araucaria*. Gothan later (1950 : 153) suggested, without further description of the cones, that the fact that they did not appear to shed their cone-scales at maturity was a character of major importance in separating the genus *Proaraucaria* : this condition has been discussed in an earlier section, where it was concluded that there is no evidence that the cones did not shed their scales, but a certain amount to suggest that they did. The second major conclusion is that the nearest related living species of *Araucaria* is *A. bidwilli*, the only species so far included in the section *Bunya* recently erected by Wilde & Eames (1952) in their taxonomic revision of the genus *Araucaria*, and found to-day only in Eastern Australia in Queensland. Most of the previous references to these fossil araucarians have compared them with the two living South American species, *A. araucana* and *A. angustifolia* ; though Darrow compared the fossil cones with *A. bidwilli*, this was not substantiated by any critical study of the vascularization or of the ligule, but she effectively demonstrated the structure of the embryo, which is similar to that in *A. bidwilli*. It is true that in the fossil species there is no evidence for dehiscence of the individual cone-scales, for no separate seeds nor empty scales have been found ; and this character is one of those on which Wilde & Eames differentiated their new section *Bunya* (1952 ; 44). But in general structure of the cone-scale and ligule, and in particular of their vascularization, there is a striking similarity between the living *Bunya* and the fossil species : indeed, the larger size of the cones of *A. bidwilli*, which may reach 30 cm. in diameter, appears to be the chief difference between the species as represented by the cones. The use of the generic name *Araucarites* for these cones, though it has taxonomic priority, is best set aside (cf. also Florin, 1940 ; 1944) : for this name is reserved for cones or branches of araucarian habit which, however, are lacking in preservation of structural details which might give final evidence justifying inclusion in the genus *Araucaria* itself. The name *Araucaria mirabilis* (Speg.) is therefore used, and the species is assigned to the section *Bunya* Wilde & Eames, the only other species of this section being the living *Araucaria bidwilli*, which is found to-day only in Queensland.

The proximity of these cones to the seedling structures already described is certainly significant, though there is no evidence of organic relationship. Tuberous seedlings are known amongst living species of *Araucaria* only in the section *Bunya* and in the South American section *Columbea*. The rarity of such a seedling habit in gymnosperms has already been noted ; and so far as records have been examined it is not found in any of the Taxodiaceae, to which the only other fertile cones in this area where the seedlings are found probably belong.

Similarly, the proximity of the cones to the leafy branches of araucarian habit which have been described as *Araucarites sanctaecrucis* may be of significance, though evidence of attachment of cones to such branches is missing ; but as will presently be shown, the foliation of the pedicel in the *Pararaucaria patagonica* seed cones does not rule out the possibility that the branches, or some of them, may have been related to this quite distinct type of cone.

Pararaucaria patagonica Wieland

(Pls. 6, 7 : Text-figs. 5–7)

1929. *Pararaucaria patagonica* Wieland, p. 60.
1929. *Pararaucaria elongata* Wieland, p. 60.
1935. *Pararaucaria patagonica* Wieland, p. 21, pls. 2–5.
1936. *Pararaucaria patagonica* Wieland : Gordon, p. 14.
1937. *Pararaucaria patagonica* Wieland : Darrah, p. 223.
1940. *Pararaucaria patagonica* Wieland : Florin, p. 36.
1944. *Pararaucaria patagonica* Wieland : Florin, p. 513, pl. 184, figs. 23–26.
1947. *Pararaucaria patagonica* Wieland : Arnold, p. 314.
1949. *Pararaucaria patagonica* Wieland : Feruglio, p. 129.
1951. *Pararaucaria patagonica* Wieland : Feruglio, p. 35.

EMENDED DIAGNOSIS. Seed cones, ovoid in shape, varying in length from 4·7 cm. to 2·3 cm. and in diameter from 2·4 cm. to 1·3 cm., borne on slender pedicels clothed with spirally arranged, imbricate, broadly lanceolate and somewhat acute leaves with longitudinal striation of the abaxial surface. Bracts bearing the axillary fertile scales usually about 38 in number in average-sized cones, large and conspicuous, probably woody, each subtending a thick fertile scale, and arranged in a closely imbricate spiral succession with angle of divergence 3/8. Bract 10 mm. long, 12 mm. wide, 1·5 mm. thick, free from fertile scale for greater part of length ; fertile scale 10 mm. long, 12 mm. wide, 2·5 mm. thick, showing longitudinal ridges on its protruding distal abaxial face, and bearing usually one large inverted seed, laterally inserted, flattened and winged, the seed separating from scale at maturity. Seed 6 mm. long, 6 mm. wide, 2 mm. thick, with wing 2 mm. wide tapering towards base and tip of seed ; testa with inner stony layer, and outer layers composing wing of a characteristic stellate sclerotic lacunar tissue. Embryo 4 mm. long, polycotyledonary ; seed probably exalbuminous.

Cone axis slender, with narrow pith and thick endarch cylinder of xylem. Succession of elements in primary xylem includes scalariform and reticulate tracheids, passing over into elements with biseriate bordered pits. Secondary xylem tracheids usually with uniseriate bordered pits, contiguous and flattened, the pit apertures rounded or ovate ; medullary rays with cross field pitting of cupressoid form. No resin ducts or cells present. Bract supply arises from axis stele as a single trace from base of leaf gap ; fertile scale supply arising as two traces, one from each side of leaf gap above bract trace, the two traces fusing to give inverted bundle, which is accompanied into the scale on the adaxial face by a large strand of sclerenchyma which forks into two. Bract and fertile scale supplies single in base, branching higher up, with an abundant transfusion tissue linking the bundles tangentially and persisting in tips of bract and scale when bundles die out. Seed supplied by a single lateral strand from supply of fertile scale.

DESCRIPTION. This species is represented by a large collection of mature seed cones ; no younger stages appear to be present, though it has been possible to section only a few of the specimens for more detailed examination. (One specimen, V. 30974, smaller than average with length 24 mm. and width 12 mm., probably represents an abortive or unfertilized cone, but preservation is not good enough for a convincing

identification.)   The species is redescribed here with special reference to a number of diagnostic characters which were not included in Wieland's original account (Wieland, 1935) ; it is the most interesting species in the collections from the Cerro Alto localities, and its relationships with other conifers have not so far been assessed by comparison of a sufficiently wide range of characters.   It may be of interest to note here that Feruglio (1949 : 129) reports, in a review of the localities where the plants of the petrified forest are known to occur, that *Pararaucaria* has been found only in two of the localities with petrified cones, viz., the Cerro Alto, where it is associated with the cones of *Araucaria mirabilis*, and near the Estancia Los Toldos, where the latter species is missing.

The general habit of the cones is illustrated in Pl. 6, figs 55, 56, 63.   They vary in length from 4·7 cm. to 2·3 cm., and in diameter from 2·4 cm. to 1·3 cm., the average size being about 4 cm. long and 2 cm. in diameter.   There is no evidence that smaller cones represent younger stages ; they probably represent attenuated cone forms, bearing fewer appendages.   This range in size corresponds with that observed by Wieland in his specimens.   A longer cone type was originally separated by him (1929 : 60) as *Pararaucaria elongata*, but later (1935 : 21, pl. 5, fig. 6) he included this type in *Pararaucaria patagonica*.   A similar long cone is shown here in Pl. 7, figs. 74, 75 ; and no other distinctive characters have been noted in it.   These long cones are often poorly preserved and much weathered, as in Pl. 7, fig. 74, but the bract and fertile scale show the same proportions as in smaller specimens.   Cones of average size as well as these long cones have been found to contain fully developed embryos in the seeds (Pl. 6, fig. 58 ; Pl. 7, fig. 75), a condition refuting Wieland's suggestion that the latter represent the mature seed cones, while the former are immature.   Such a range in size is a feature quite common in the cones of, for example, living species of *Pinus*.

The cones are somewhat ovoid in shape ; many show marked unilateral weathering of the surface features and some a varying degree of compression.   The specimen in Pl. 6, fig. 63, approaches most nearly to the condition of the surface features in the living plants.   A number of large and conspicuous bracts (*b*), about thirty-eight in an average-sized cone, are arranged in a close-set spiral around the axis, with successive bracts overlapping and with an angle of divergence of 3/8 as in other cones observed.   In the axil of each bract is the fertile scale (*f*), showing slight longitudinal ridging of the abaxial surface, where it protrudes distally. Towards the cone apex the bracts and fertile scales diminish rapidly in size (Pl. 6, fig. 56), the topmost members being sterile (cf. series of sections V. 30965, V. 30968). In some cones there is a markedly acute tip (Pl. 6, fig. 56), in others it is more blunt (Pl. 6, fig. 55).   Only two specimens among the cones have been found attached to their pedicels : Pl. 6, fig. 62, shows one of these, and clothing the pedicel is an overlapping spiral series of broad, flat, lanceolate leaves, as seen in more detail in Pl. 6, fig. 64.   These leaves are regularly striated on the abaxial surface ; the furrows may represent the position of lines of stomata, but it has not been possible to verify this from structural detail in either sections or cuticles.   Another feature of some diagnostic interest is also illustrated by this specimen : it shows a sharp transition from the sterile leaves to the bracts and fertile scales at the base of the cone, a

character noted, for example, by Seward & Ford (1906 : 354) as one offering a marked distinction between the Araucariaceae and the Pinaceae, the transition in the former being much more gradual.

The narrow cone axis is seen in transverse section of the basal region of a cone in Pl. 7, fig. 65, and shows a relatively narrow pith and thick cylinder of xylem : the xylem diminishes in thickness towards the tip of the cone. The pith includes large scattered cells with dark brown contents : the stele is endarch, with scanty primary xylem and a wide zone of secondary xylem with regular radial files of tracheids, without parenchyma and without resin ducts or cells, and with unseriate secondary medullary rays. The structure of the xylem is illustrated in more detail in Pl. 7, figs. 66–72. The centrifugal succession of elements in the primary xylem is shown in radial longitudinal section from right to left in Pl. 7, figs 66–68. Annular tracheids cannot be identified with certainty ; but a succession of spiral elements, in which there is some evidence for the formation of bordered pits between the turns of the spiral band (Pl. 7, fig. 67, s.p.), is followed by widely reticulate tracheids (Pl. 7, fig. 67, ret.) and these are succeeded, in the base of the cone, by tracheids with biseriate alternating bordered pits (Pl. 7, figs. 70, 71, bi.), probably belonging to the secondary xylem.

Beyond these come the tracheids forming the bulk of the woody cylinder ; these have uniseriate bordered pits on the radial walls (Pl. 7, figs. 68, 69, 70, sec.). The pits are usually contiguous, with flattening of the pit outline in the area of contact (fig. 69) : the form of the pit apertures varies from rounded to oval. Parts of the medullary rays are seen in radial longitudinal section in Pl. 7, figs. 68—70, 72 (m.r.) The rays are 1–5 cells high and ray tracheids have not been observed. The cross-field pitting is fairly constant (Pl. 7, fig. 72), there being 2–4 horizontal rows of rather small pits, which are of markedly " cupressoid " form (cf. Phillips, 1941: 267).

These characters of the xylem, not noted by Wieland, may most conveniently be discussed here : they represent features which have been widely used in the past as a means of identifying conifer woods.

Bailey has recently re-emphasized the comparative significance of the primary developmental succession in the xylem of gymnosperms (Bailey, 1949, 1925 ; cf. also Florin 1936, 1937) ; and in *Pararaucaria* the sequence which has just been noted appears to be intermediate between that found in the " lower " gymnosperms (Cycadales, Cordaitales) and that in the " higher " gymnosperms (Coniferales, Ginkgoales, Gnetales). In the former groups scalariform elements are present and are succeeded by reticulate elements, and these by elements with the typical bordered pits of the metaxylem and secondary xylem ; bordered pits are not formed in the spiral tracheids, where, however, they do appear in the shortened succession found in the xylem of the latter groups, where scalariform and reticulate forms are usually absent. In *Pararaucaria* the presence of reticulate tracheids in the succession is comparable with the similar condition noted by Bailey (1925 : 593) as occurring sporadically in *Araucaria* and *Agathis*, which he has interpreted as intermediate between " lower " and " higher " gymnosperms in this respect. Though it is true that Bailey's observations were made on stem wood and the condition in *Pararaucaria* is

reported from the cone axis only the comparison is worth recording, though fuller knowledge of developmental sequence in the cone axes of the various groups is not available for comparison.

The structure of the secondary xylem, in particular the radial pitting of the tracheid walls and the cross-field pitting of the secondary medullary rays, has often been used as a comparative basis for assessing relationships in coniferales. The variability in form and arrangement of tracheid pitting which has been demonstrated in stem and root wood in individual plants in a variety of families of the Coniferales is, however, such that the xylem type in the *Pararaucaria* cones might be included within the range found, for example, in *Pinus*, *Sequoia*, or Araucariaceae (Bailey, 1933 ; Bailey & Faull, 1934 ; Pool, 1929). Cross-field pitting in stem and root wood is also a variable character (e.g., Bannan, 1944). Cupressoid form of the pits in the cross-field is found fairly regularly in the Araucariaceae and Cupressaceae, and it also occurs amongst the Podocarpaceae, Taxodiaceae, Taxaceae, and even occasionally in the Pinaceae (cf. Phillips, 1941 : 268, 274–277). The condition in the Araucariaceae and in *Taxodium*, where the cupressoid cross-field pits may be as numerous as in *Pararaucaria*, probably conforms most nearly with that in the fossil cones. But details of cone-axis wood are available for comparison in very few cases : in *Araucaria* the records given by Thomson (1913, pl. 4, fig. 34) are of multiseriate pitting of the radial tracheid walls of typical araucarian form. This, together with the very wide pith and narrow ring of xylem (Thomson, 1913 : 4, pl. 1, figs. 5, 7) serves readily to distinguish araucarian cone axes from those of *Pararaucaria*. No satisfactory direct comparison with cone axis structure of other families of conifers can be made without further investigation of these. The evidence of the cross-field pitting taken from stem wood structure would, however, tend to favour a reference of the fossil cones to relationship with the Taxodiaceae, where too the same type of tracheidal pitting has been demonstrated in the root of *Sequoia semper-virens* (Bailey & Faull, 1934, pl. 103, fig. 29). [See note on p. 138].

The mode of attachment of the vascular supply of the bract and fertile scale to the axis stele is illustrated in Text-fig. 5, A–D, which is taken from a series of sections at intervals of approximately 2·5 mm. apart, in the basal half of a cone, and viewed from the base upwards. It has not been possible to follow out the course of the bundles from a series through a single leaf-gap : but the vascular supply may be interpreted from a number of gaps cut at varying levels. The bract supply (*b*) comes from the base of the leaf-gap as a single strand, being separate in origin from the supply of the fertile scale, which is derived as two separate strands (Text-fig. 5A, *f*^{1}, *f*^{2},) from the sides of the gap above the bract supply ; these two strands subsequently fuse to give one large bundle (Text-fig. 5, B–D, *f*) after each has undergone torsion through 180°, so that the protoxylem comes to lie on the outer (abaxial) face of the fusion bundle (*f*), which is thus inverted alongside the bract supply (*b*) in the cortex ; the phloem is not preserved. This is also illustrated in Pl. 6, figs. 57, 58, (*b.s.*, *f.s.*). A striking feature, though of subsidiary comparative interest, is the bulky strand of sclerenchyma which accompanies the inverted vascular supply of the fertile scale on its adaxial face (Pl. 6, figs 57, 58, *sc.*; Text-fig. 5, stippling). This strand, which has its origin in the cortex in the angle above the leaf-gap, forks

into two as the fusion bundle passes out of the cortex into the base of the fertile
scale, and the paired strands remain a prominent feature in the fertile scale for about
half its length (Text-fig. 6).

This account of the origin of the bract and fertile scale supplies does not agree
with that of Wieland. He has described, from cut surfaces of cones, the origin of
the bract-fertile scale supply as a " single heavy concentric strand " (1935 : 22, pl. 4,
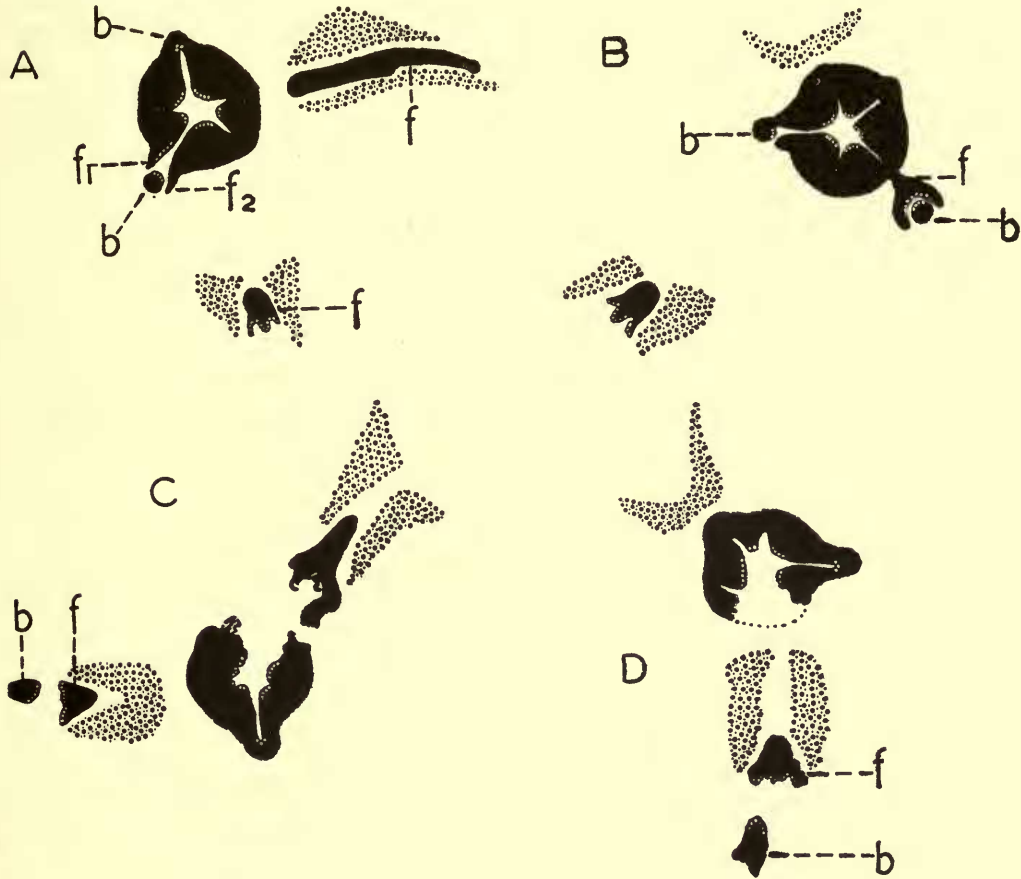
TEXT-FIG. 5. *Pararaucaria patagonica* Wieland. Transverse sections of stele of cone
axis from below upwards, to show detachment of bract supply (*b*) and fertile scale
supply (f_1, f_2), from leaf-gaps. The two traces f_1, f_2 of the fertile scale supply fuse with
inversion to give a single bundle (*f*). Xylem black, with protoxylem white; scleren-
chyma of fertile scale in double stippling. V. 30964 *c–f.* × 6·7.

fig. 3 ; pl. 5, fig 5). He nevertheless interpreted this condition as being in exact
agreement with that in *Pinus*, where however, according to the account of Aase
(1915), the bract trace is normally in its origin quite free (except at the cone base)
from the fertile scale supply, as indeed is the case in others of the Pinaceae which
have been examined (e.g., Aase, 1915 ; Radais, 1894). According to the observa-

tions on which the present description is based, *Pararaucaria* does resemble the Pinaceae in this respect, as also the section *Bunya* of *Araucaria*, and some of the Taxodiaceae (Aase, 1915 : 294–7) ; and it has not been possible to confirm Wieland's observations. In his pl. 4, fig. 3, the supplies to the bract and fertile scale are clearly separate but in his pl. 5, fig. 5, there is some evidence that a single strand is present in the cortex outside the leaf-gap : this latter condition, however, is in the cone base, and such a condition has been noted by Aase (1915 : 282–5, 296) as occurring in the base of *Pinus* and *Cryptomeria* cones, though the normal condition higher up is to find the bract and fertile scale supplies quite separate in origin.

The external features of the bract and fertile scale at the cone surface have already been noted : Pl. 6, figs. 57–60 and Text-fig. 6 show their structure in series of tangential longitudinal sections in sequence from inside outwards. The most conspicuous characters are the thick, persistent and probably woody bract (*b*), subtending the thick woody fertile scale (*f*), which bears on its upper surface a single large, inverted seed, which is flattened and winged. The bract is free from the fertile scale for the greater part of its length, and is fused with it only towards the base (Pl. 6, figs. 57–60 and Text-fig. 6). Here the double vascular supply, with the upper bundle (*f.s.*) inverted and accompanied by the two strands of sclerenchyma, is a prominent feature. The lower bundle, which supplies the bract, is single below but forks about half way up the free part of the bract, and the thick, protruding tip of the latter is supplied by a number of small vascular strands linked tangentially by a bulky tissue composed of isodiametric pitted cells, which may be described as a transfusion tissue (Pl. 6, figs. 59, 60, and Text-fig. 6, *TT*). A curious feature of the bract as described by Wieland was that it was " pleated " (Wieland, 1935, pl. 4, figs. 4, 5). His illustrations show this in respect of one flank only of the bracts, and not in all of them. Closer examination of his figures and of the sections of the series here described has provided evidence (cf. Pl. 6, fig. 57) that this apparent lateral forking or pleating is found only in the bracts cut in inner tangential planes just outside the region where they are attached to the outer cortex of the axis. Here they are so close-set that the margins of their bases tend to be laterally confluent where they overlap, so that a kind of reticulum is formed on the surface of the axis. This is not necessarily a characteristic feature, but one correlated with the closely imbricate succession of the bracts : it is certainly not one characteristic of the free distal region of the bract.

The fertile scale (*f*) is of similar size and thickness to the bract, and is also supplied in its basal region by a single vascular strand (*f.s.*) which remains unbranched until a short distance behind the distal attachment of the seed to the scale. Here it forks into 3–4 strands, and one of these, a lateral strand, passes up to supply the seed in the region of the basal foramen (Pl. 6, fig. 59, and Text-fig. 6F, *f.s.l.*). Above the insertion of the seed the vascular strands supply the prominent tip of the fertile scale ; and here too there is a well-marked transfusion tissue as in the bract. The conspicuous strands of sclerenchyma noted in the base of the fertile scale fade out about half-way up the scale : their function may have been connected with the separation of the seed scales at maturity to liberate the seeds. Though the epidermal and hypodermal tissues of the scale in this region are poorly preserved, there

is some evidence (Pl. 6, fig. 60, and Text-fig. 6H) of a grooved abaxial surface on the exposed distal face of the scale, possibly a natural feature, and one which has been noted externally as giving a longitudinally ridged appearance in a few of the best preserved cones (Pl. 6, fig. 63).
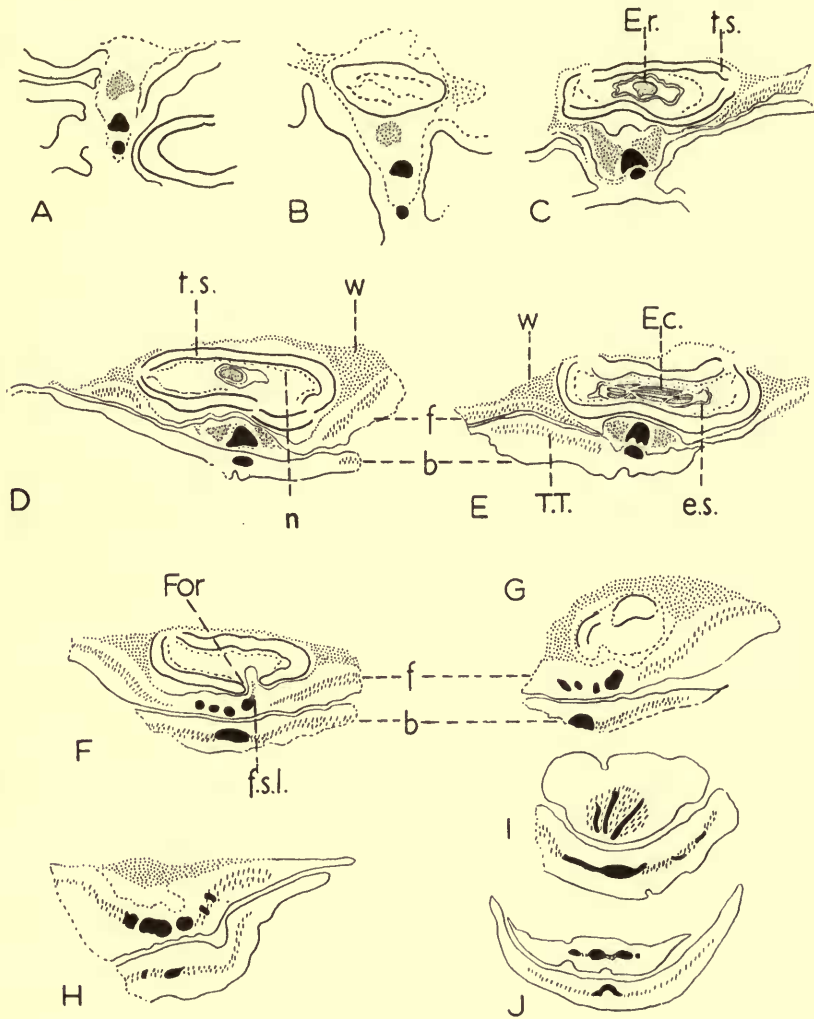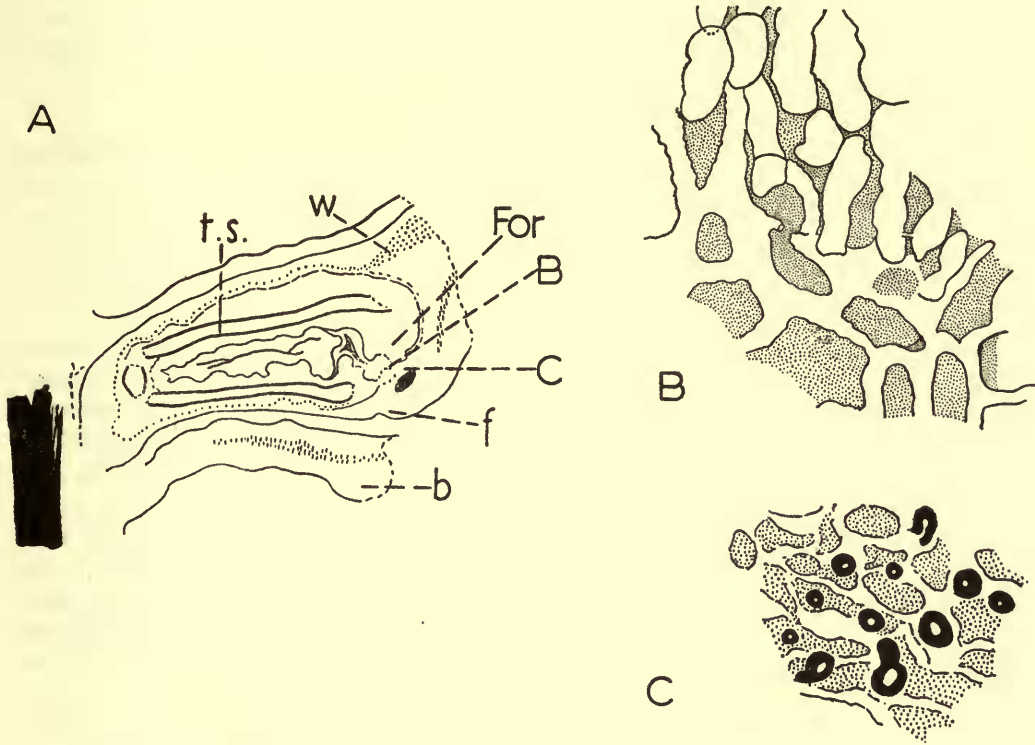

TEXT-FIG. 6. *Pararaucaria patagonica* Wieland (cf. Pl. 6, figs. 57–60). Tangential longitudinal sections of fertile scales (*f*) with seed, and bracts (*b*), taken from base outwards. (J = transverse section.) Xylem black, sclerenchyma of fertile scale double stippled, stellate sclerotic wing tissue (*w*) of testa single stippled, transfusion tissue (*TT*) stroked. *For.* = foramen of seed, *fsl* = lateral bundle of fertile scale supplying seed, *ts* = stony later of testa, *Er* = radicle of embryo, *Ec* = cotyledons of embryo, *e.s.* = ? embryo sac, *n* = ? nucellus. (A, B, V. 30959 *c*, *e* ; C–G, V. 30961 ; H, I, V. 30960*a* ; J, V. 30945*a*). × 5.

The seeds themselves are large and flattened ; the latter feature appears to be general and may be a natural character. The usual condition is to find one seed per scale, inverted and with its basal attachment and vascular supply lateral as shown in Pl. 6, fig. 59 and Text-fig. 6F. Wieland reported one cone only in part of which he found 2 seeds per scale, but this condition appears to be exceptional (Wieland, 1935 : 22). All the cones examined appear to be mature ; fully formed embryos are found preserved in the seeds of some of the cones sectioned, and the micropyles, directed towards the cone axis, are sealed (Pl. 7, fig. 73). The seeds at first sight appear to be embedded in the tissue of the fertile scale on its upper surface ; but closer examination shows that this is not the case. There is a conspicuous " stony " layer in the testa (Pl. 6, figs. 57–59, Text-fig. 6, *t.s.*), consisting of a deep zone of elongate, thick-walled cells lying with their longer axes at right angles to the surface. This layer is continuous except for the basal foramen in the region where the seed is attached. The stony layer is surrounded by an outer layer, confluent on either side of the seed body with a flattened wing (Pl. 6, figs. 57–60 and Text-fig. 6, *w*), which consists of a characteristic lacunar tissue of stellate, thick-walled cells or sclereids (Pl. 6, fig. 61), like the " cellules étoilées " of Radais (1894 : 231) in his description of the wings on the seeds of *Abies*. This tissue, resembling an aerenchyma, is markedly different from the tissue of the fertile scale below, to which it is closely adpressed. It corresponds exactly with the tissue described by Radais (1894 : 231, pl. 4, fig. 47) and von Tubeuf (1892 : 205, text-fig. 18) in the wings of the seeds of the Pinaceae, where, in the earlier stages of development, the whole of the inner surface of the seed, including the wing, is attached to the upper surface of the fertile scale, and separation only takes place at a later stage as the seed matures. The evidence from the specimens of *Pararaucaria* here examined, which have all been mature, suggests that the seed, including the wing, is separate from the surface of the scale, except in the region of attachment at the basal foramen (Pl. 6, figs. 57–59 and Text-fig. 6). Text-fig. 7 illustrates the relationship of the seed to the scale in this region : and it can be seen that there is an " absciss " zone here consisting of an aerenchyma-like tissue continuous into the foramen, suggesting that at maturity there is rupture of the tissue in this stalk-like region. This rupture would finally liberate the ripe seed. Without younger stages, it is hardly possible to decide whether the outermost " wing " of the seed coat is at an earlier stage attached to the scale, as in the living Pinaceae, or free from it, as in the living *Agathis* (where the single seed is median) and some of the Taxodiaceae with inverted winged seeds (*Taiwania*, *Taxodium*). This point, though a critical one, must remain undecided. Wieland's specimens were probably also mature and clearly show the separation of this wing (Wieland, 1935, pl. 4, fig. 5, pl. 5, fig. 2) which he did not recognize when he interpreted the condition of the seeds as comparable with that in *Araucaria*, " inclosed by the drooping curtain-like, expanded, and flattened and coalesced tip of the seed scale " (p. 22). It was principally on the basis of this feature, associated with the *single* seed, that he drew his comparison with the genus *Araucaria*, and instituted the name "*Pararaucaria*" to emphasize the intermediate nature of the genus; for he interpreted the slender cone axis and narrow pith as pinacean characters, together with the more or less free bract (p. 23). Florin, however,

described Wieland's " curtain-like" structure as the sarcotesta of the seed coat (1944 : 513), though he did not recognize the seed as winged.

The tissues of the seed inside the stony layer of the testa are poorly preserved in most specimens : but Pl. 6, figs. 57, 58 and Text-fig. 6, c, e, illustrate a cone in

TEXT-FIG. 7.   *Pararaucaria patagonica* Wieland.   A. Longitudinal section of fertile scale (*f*) and bract (*b*) of cone, cut to one side of median plane to show foramen of seed (*For.*) in region of attachment to scale.   *ts* = stony layer of testa, *w* = wing tissue of testa : xylem of cone axis and fertile scale shown in black.   V. 30966*a*.   × 6·7. B. Tissue shown at *B* in foramen of seed in fig. A.   × 240.   C. Tissue shown at *C* in fig. A.   × 240.   In B and C, intercellular spaces stippled, thick-walled ? fibrous cells in solid black.

which embryos were preserved.   The remains of the embryo sac are probably represented at *e.s.*, and of the nucellus at *n*.   The embryo is seen cut transversely in the region of the radicle towards the micropylar end of the seed in Pl. 6, fig. 57. and Text-fig. 6, c, and in the region of the cotyledons, towards the base of the seed, in Pl. 6, fig. 58, Text-fig. 6, e.   There are several (probably eight) cotyledons.   Pl. 7, figs. 73, 75 show an embryo in radial longitudinal section in another cone, with the radicle tip (*r*) pointing towards the sealed micropyle (*m*).   This is the only specimen in which it has been possible to demonstrate an embryo in median longitudinal section

to confirm the orientation.   In Wieland's account (1935 : 22) he refers to a suggestion of a dicotyledonous embryo, but the preservation of his specimens left this point inconclusive.

Butts & Buchholz (1940) have shown that in the Pinaceae, polycotyledonary embryos with cotyledons reaching nine in number are a characteristic feature, while in the Taxodiaceae, the number varies among the genera from 8 to 2.   But in the remaining families of the conifers embryos with 3 or more cotyledons do occur in certain genera, though the usual number is 2, so that the character has a limited diagnostic value.

RELATIONSHIPS

The chief features of *Pararaucaria patagonica* here described which were not noted by Wieland (1935) in his account of the species are : the foliation of the pedicel ; the details of the wood structure ; the detachment of the bract trace from the cone stele separately from the two traces which form the supply of the fertile scale ; the winged, detachable nature of the inverted seed and its lateral position ; and the polycotyledonary embryo.

Wieland's account established the characters of slender cone axis with narrow pith, and the conspicuous bract scales of the cone bearing in their axils the large fertile scales each normally with one large inverted seed, which he interpreted as being enclosed in the scale tissue.   On this association of characters he assessed the systematic position of the genus as intermediate between Pinaceae and *Araucaria* (Wieland, 1935 : 23), and accordingly instituted the generic name *Pararaucaria*. A re-analysis of the relationships of the genus is attempted in the following table on the basis of the fuller set of criteria of comparison which can now be used.   The available characters of the petrified cones which might be suitable for giving a quantitative index of aggregate intergeneric differences are too few in number for effective use : but the table summarizes the position qualitatively.

Pararaucaria patagonica Wieland, emend.

List of Characters used for Comparison with some other Coniferales,
Numbered for Reference as in Table below.

1. Bract free from fertile scale for greater part of length.
2. Bract large and conspicuous at maturity.
3. Bract trace distinct in origin from traces of fertile scale.
4. Usually one seed per fertile scale.
5. Seeds inverted.
6. Seeds attached laterally.
7. Seeds winged.
8. Seeds free throughout development from fertile scale, except in region of basal foramen.
9. Several cotyledons (> 4) in embryo of seed.
10. Cone axis slender, with narrow pith in stele.
11. Secondary medullary rays of cone axis wood with pits of cross-field cupressoid and numerous.

TABLE SHOWING POSITIVE CORRELATIONS WITH SOME FAMILIES AND GENERA OF CONIFERALES.

Characters compared numbered as in list above.
+ = positive correlation in all species described.
⊕ = positive correlation in some species described.
? = doubtful or undescribed character.

	Characters of bract, fertile scale and seed.									Cone axis	
	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.
Pararaucaria	+	+	+	+	+	+	+	?	+	+	+
Araucaria	..	+	⊕	+	+	?	..	..	..	..	+
Agathis	..	+	..	+	+	..	+	⊕	..	..	+
Pinaceae	+	..	+	..	+	+	+	..	+	+	..
Taxodiaceae	..	+	⊕	..	⊕	+	⊕	+	⊕	+	⊕
Romeroites	..	+	?	..	..	?	..	+	?	+	?
*Cheirolepidaceae	⊕	⊕	?	..	+	+	..	..	?	?	?
*Pseudo-Araucaria	..	?	?	..	?	+	..	..	?	?	?

* The data for these fossils, which superficially bear some resemblance to *Pararaucaria*, are taken from the accounts given by Spegazzini (1924 : *Romeroites*), Hirmer & Hörhammer (1934 : Cheirolepidaceae), Fliche (1895 : *Pseudo-Araucaria*). A revision of the characters in all these types, especially of the relationship between seed and fertile scale, is necessary before any critical systematic comparison with *Pararaucaria* can be made.

It will be seen on summation of positive correlations that the nearest comparison is with the Taxodiaceae (*sensu* Pilger, 1926 : 342), which shows the greatest number of positive correlations. Even allowing for uncertainty on criterion (8) in *Pararaucaria* (freedom of seed from scale throughout development), the comparison with the Taxodiaceae is closer than with the Pinaceae, for on criteria (2) and (11) (large size of bract ; and cross-field pits numerous, cupressoid) the conditions found in *Pararaucaria* and amongst the Taxodiaceae do not characterize the Pinaceae : and on criteria (1) and (4) (degree of freedom of bract from fertile scale, and number of seeds per scale), which represent the chief differences between *Pararaucaria* and the Taxodiaceae, it may be noted on (1) that in *Cryptomeria* (and probably also in the Jurassic genus *Elatides*) in the Taxodiaceae there is a form intermediate in respect of degree of fusion of bract and fertile scale, and on (4), that in *Taiwania* in the Taxodiaceae a single seed instead of two may sometimes be found, while in *Pararaucaria* the two-seeded condition has abnormally been found. In these two respects *Cryptomeria* and *Taiwania* respectively may be regarded as intermediate between the *Pararaucaria* condition and a more typical taxodiaceous condition.

Certain features of *Pararaucaria* have been omitted from the lists above as not affording sufficiently reliable distinctions : these are the foliation of the pedicel, the sharp transition from the foliation of the pedicel to the bracts and fertile scales of the cone itself, the size of the cones and the number of cone-scales per cone, the radial pitting of the tracheid walls, and the vertical ridging of the fertile scales. But it may be noted that in each of these features correspondence with characters occurring amongst the Taxodiaceae may be found. In the case of the radial pitting

of the tracheids, reference may be made to the range of variability in xylem structure demonstrated in the Redwood, *Sequoia sempervirens*, by Bailey & Faull (1934, pl. 103, fig. 29), where the condition in the fossil cones is found in secondary xylem of root.   The vertical ridging of the fertile scale is, so far as I am aware, a feature characteristic of the Taxodiaceae in the genera *Sequoia*, *Sciadopitys*, and *Taxodium*, though in the first two of these it is also found to some extent in the bract.   Finally, the general "habit" of the cones is taxodiaceous ; the proportion of bract to fertile scale, the size of the cones, the vertical ridging of the fertile scale, all combine to give a habit which on superficial examination one would tend to refer to the Taxodiaceae.

In the analyses just given, the Taxodiaceae are referred to in the sense of Pilger's definition (Pilger, 1926 : 347) ; the family in this widely-defined sense shows considerable diversity in certain characters, e.g., the orientation of the seed, and the number of the cotyledons.   The probably heterogeneity of the Taxodiaceae in this inclusive sense has, however, been generally recognized : Pilger himself separates the genera into two sub-families and a number of sub-groups, while Hayata (1932) arranged the genera of Pilger's group in a number of separate families.   Florin has more recently re-examined the relationships of the Taxodiaceae, *sensu* Pilger, (Florin, 1931 : 484–491 ; 1940 : 78).   He agrees (1931 : 490) with Pilger's classification, whilst admitting it may be artificial, since it deals with a family intermediate in its general characters between others more sharply defined : but at the same time he has re-emphasized its diversity and probable heterogeneity.   In particular, he draws attention, amongst other distinctive features, to the characteristic epidermal characters of the Tasmanian genus, *Athrotaxis*, which can readily be used to distinguish it from other genera of Taxodiaceae in the northern hemisphere.

In view of this diversity in the Taxodiaceae, *sensu latu*, *Pararaucaria* may meantime most conveniently be referred to this family.   It most nearly resembles *Taiwania* in the one-seeded condition, *Cryptomeria* in the condition of the bract in relation to fertile scale, and *Sequoia* and *Taxodium* in the polycotyledonary embryo, but resembles no one living genus in its combination of characters.   The possibility remains, however, that the seed and its wing may have been attached, in earlier stages of development, to the fertile scale as in the Pinaceae : and in this case the most natural position would be to place *Pararaucaria* in a separate new family of Coniferales, intermediate in position between the Taxodiaceae and Pinaceae.   In a recent review by Takhtajan (1953) the phylogeny of the Taxodiaceae has again been discussed, and he suggests that they probably originated from the earliest and most primitive Pinaceae, though no fresh evidence is adduced in support of this view.

Wieland (1935 : 24) referred *Pararaucaria* to the fossil family Cheirolepidaceae as defined by Hirmer & Hörhammer (1934 : 79) : but this reference was based on the assumption that the seed was borne in the scale tissue as in the genus *Araucaria*, and as has already been demonstrated, this is not the case.   Florin (1940 : 36 ; 1944 : 513) suggested that *Pararaucaria* might be identical with the South American fossil genus *Romeroites*, from the province of Neuquen.   This genus, as described by Spegazzini (1924 : 134), is undoubtedly taxodiaceous, but differs from *Pararaucaria* chiefly in the thin, many-seeded fertile scales with seeds upright and fleshy,

and fusion of bract with fertile scale for the greater part of its length. A more detailed description of this genus is undoubtedly desirable, but according to Spegazzini's account it does not correspond with *Pararaucaria*, though the size of the cones and the general external habit are somewhat similar. Gothan (1950 : 153) in a very brief note recognized that *Pararaucaria* had nothing to do with *Araucaria*, and accordingly indicated that the genus was misnamed: but he gave no further description of the cones nor indication of their true relationships, of which, as has been shown, no more satisfactory definition can be given unless younger stages in the development of the cones are found.

DISCUSSION

The chief interest of these conifers of the Cerro Cuadrado forest lies in their relationship with other conifers and their geographical distribution.

Araucaria mirabilis is an extinct species, and appears to have its nearest living relation in the Queensland " bunya bunya," *A. bidwilli*, and not in *A. araucana* or *A. angustifolia*, the only living species of *Araucaria* in South America ; but it might be considered to represent an ancestral form of these, if the wings of the cone scales had become reduced in the evolution of the species. This view on the evolution of the South American living araucarians has already been expressed by Darrow (1936 : 333). The South American fossil records (cf. Florin's review, 1940 : 33–40) do not include any which furnish critical evidence of the wingless cone scales of species of the section *Columbea* Endlicher, emend. Wilde & Eames : the cone scale from the (?) Upper Cretaceous of the Cerro Guido in Santa Cruz, which was named *Araucarites patagonica* by Kurtz (1902 : 49) and referred to as comparable with the living *Araucaria brasiliensis*, was not figured, and was an incomplete specimen described as representing the lower part of the scale. Other cone scales in the form of compressions, from Meseta de Baquero in Santa Cruz, have also been referred to the section *Columbea* (Feruglio, 1951 : 65). These are more or less incomplete and are not illustrated, but from the description and from their comparison by Feruglio with Berry's cone scales of *Araucaria* from the nearby Gran Bajo de San Julian (Berry, 1924 : 480, text-figs. 2, 2a) it appears that they are winged scales. Berry refers to his as " obviously thick and woody," which suggests that they may have belonged to the section *Bunya* Wilde & Eames though they are much smaller than those of the living *A. bidwilli*. Other seed scales, which he also compared with Berry's, were described by Feruglio as *Araucaria* (Feruglio, 1951 : 39), from the Gran Bajo de San Julian, and they too might have belonged to the section *Bunya*. Both Berry's and Feruglio's seed scales come from localities in the region of the same volcanic complex (the porphyritic series of the Bahia Laura), which Feruglio has dated as of age mid-Jurassic to Wealden (1951 : 74), and which also contains the petrified forest around the Cerro Alto ; but it is unlikely, owing to the incomplete preservation of the compressed cone scales, that any close comparison can be made between them and the petrified cone scales of *Araucaria mirabilis* in the forest, though they are not dissimilar in size and general form. Feruglio does not believe that the San Julian specimens are identical with *Araucaria mirabilis*.

There is, therefore, as yet no critical record of wingless cone scales in South American fossil floras. The evidence so far provided from sterile shoots with broad flat leaves might indicate araucarians of the sections *Bunya* Wilde & Eames, *Intermedia* White, or *Columbea* Endlicher emend. Wilde & Eames ; and petrified woods have not yet provided reliable evidence for distinction of these sections. The South American records are, however, relatively scanty, and the absence from them of critical evidence of fossil species of *Columbea, sensu* Wilde & Eames, is necessarily inconclusive for assessment of the age of this section on the South American continent in comparison with that of species of the section *Bunya*, of which *A. mirabilis* is the only fossil form with critical structural evidence of relationship. Wingless araucarian cone scales are rare in the fossil records of the Southern Hemisphere as a whole (Florin, 1940 : 27), but they have been reported from the Jurassic of Australia and New Zealand (*A. grandis* Walkom, 1921 : 13, pl, 3, fig. 6 ; Edwards, 1934 : 100), suggesting that they may have been as ancient as the winged types, which are abundant in Jurassic rocks, and indicating that they did occur in Mesozoic times in Australasia, where they are now extinct The evidence, therefore; though scanty, does not support the attractive hypothesis of the South American evolution of *Columbea* ; and accordingly, *A. mirabilis* probably bears no direct relationship to the living South American species, but represents an extinct element of an earlier more widespread araucarian flora, some of the species of which have disappeared. The presence of such a type as *A. mirabilis* in South America, however, does provide another link between the floras of Australasia and South America. *A. mirabilis* may well have been a member of the parent stock from which the modern " bunya bunya " of Queensland sprang, a stock more widely spread than its descendents ; but in the development of the South American floras it eventually died out, while the species with wingless cone scales persisted there to the present day. Araucarians belonging to the Australasian sections *Eutacta* or *Intermedia*, with wide, thin, papery wings on the seed scales, were also represented in earlier South American floras ; perhaps the best evidence for this is provided by *Araucaria pichileufensis*, described by Berry from Rio Pichileufu in Territory of Rio Negro (Berry, 1938 : 59, pl. 11, fig. 1). This is a Tertiary species, though its exact age is doubtful (Florin, 1940 : 39), and might suggest that either section *Eutacta* or *Intermedia* persisted longer before extinction on the South American continent than did *Bunya*, though critical records are too scanty for such a generalization to be made at this stage. Florin has renewed the emphasis on the part probably played by Antarctica, whether as an intercontinental land bridge along which migration could take place, or as the place of origin of some of the southern genera (Florin, 1940 : 85–6, 92) : and the distribution of fossil and living species of *Araucaria* in South America and Australasia supports this hypothesis.

Pararaucaria patagonica represents an extinct genus and presents a different problem in distribution. The Taxodiaceae, which probably represent the nearest living relations of this genus, are to-day confined to the northern hemisphere, with the exception of *Athrotaxis*, with three species living in Tasmania. The only other fossil records of this family from the southern hemisphere are three species of *Athrotaxis*—*A. ungeri* (Halle) from the Mesozoic (possibly Lower Cretaceous) of Southern

Patagonia, and two other species from the Cretaceous of New Zealand and the Tertiary of Tasmania (Halle, 1913 : 40–44 ; Florin, 1940 : 35, 77)—and *Romeroites argentinensis* Speg. (Spegazzini, 1924 : 134–9), from Neuquen, South America (? Upper Jurassic or Cretaceous). Florin has, however, drawn attention to the separate and peculiar nature of the genus *Athrotaxis*, and has suggested that it may represent a distinct, though probably remotely related, line of descent from the Taxodiaceae. *Pararaucaria* adds, then, to the evidence for an earlier more widespread distribution of taxodiaceous types of plant in the southern hemisphere ; along with *Romeroites*, it is now extinct, while *Athrotaxis* has disappeared from South America. *Pararaucaria* is the only genus related to the Taxodiaceae which shows freedom of bract from fertile scale for the greater part of its length, and so might be regarded as an earlier member of an evolutionary series of forms leading to some of the modern Taxodiaceae where fusion is more or less complete. Such an interpretation would place *Pararaucaria* in line with that of Florin for the evolution of the coniferalean ovulate strobilus, where he regards the cohesion of the bract with its axillary seed scale complex as a condition derivative from more primitive forms where they are free. However, the Taxodiaceae (*sensu* Pilger) are an ancient and widespread family in the northern hemisphere ; among living genera, *Sciadopitys* is already known in the Jurassic, and other genera are abundant in younger rocks, especially in the Tertiary. Hirmer has however (1936 : 65), also included the much older Upper Permian *Pseudovoltzia*, the Triassic *Voltzia* and the Rhaeto-Liassic *Swedenborgia* in this family : in the two former genera, the bract and ovuliferous scale are more or less free, and in the latter are partially fused. Lack of critical evidence for the exact geological age of *Pararaucaria* precludes close phyletic comparison with other taxodiaceous genera : but as already indicated (p. 102), the most recent evidence places the age of the petrified forest as at some stage between mid-Jurassic and Wealden. The characters of *Pararaucaria* itself certainly support the assignation of Mesozoic rather than Tertiary age, for in younger floras the majority of the genera are modern, and *Pararaucaria* cannot be closely compared with any living genus. A reference made by Wehrfeld (1935) to wood of palms in the Cerro Cuadrado floras has never been substantiated ; and the genus *Araucaria*, as represented by the extinct *A. mirabilis* in the same flora, is itself an ancient one, dating back to the Jurassic. It is probable that *Pararaucaria* represents an extinct offshoot from some common earlier stock of the Taxodiaceae, no doubt of northern origin, which underwent separate evolution south of the equator, as suggested by Florin for the case of *Athrotaxis*, rather than a type to be regarded as directly ancestral to any of the living genera.

The unique one-seeded fertile scale of *Pararaucaria* is a striking case of homeotic similarity with the condition found in many other conifers of the southern hemisphere —*Araucaria, Agathis,* and the Podocarpaceae, where distribution of the single seed is associated with the entire woody cone-scale, separate winged seed and entire cone-scale with fleshy developments respectively. Biologically, the closest comparison in this respect with *Pararaucaria* is with *Agathis*, where there is also a single winged seed, but with median insertion on a single cone-scale representing the completely fused bract and fertile scale. In the living northern Coniferales (ex-

cluding Taxales) the cone-scales are normally two to many-seeded, with detachable seeds, though in the taxodiaceous genus *Taiwania*, which usually has two winged seeds per scale, one of these is frequently missing and the condition is similar to that in *Pararaucaria*. This modern condition in the northern Coniferales is in contrast with that amongst the oldest northern conifer floras of the Upper Carboniferous and Permian, where two of the most widespread genera, *Lebachia* and *Ullmannia*, had one-seeded seed-scale complexes. This condition disappeared relatively early in the history of northern conifers; though the Araucariaceae are notable exceptions during the Mesozoic in northern lands, they too disappeared from northern floras during early Tertiary times. In any case, this family may have had its origins in the southern continent and have spread northwards, though final proofs of this are lacking (Florin, 1940 : 78–82, 90). However, little is known of the early history of the southern floras ; and in them the one-seeded cone scale may in some cases represent, as seems probable in *Pararaucaria*, the result of reduction in number of seeds on the fertile shoot, rather than the retention of a primitive character.

There is no evidence that the possession of a single seed per seed-scale complex has conferred any special biological advantage amongst southern conifers, except in so far as it has made possible, in the genus *Araucaria*, the distribution of the single seed still associated with the protective cone-scale tissue in fruit-like fashion, simulating the samara or nut of angiosperms ; a somewhat similar condition is found in Podocarpaceae, in association with fleshy developments. In these two families a condition analogous in some respects with angiospermy has thus been attained, and the corresponding increase in degree of protection of the seed might in some measure account for the success of these two families. But in *Agathis* and *Pararaucaria* no such additional protection is associated with the single-seeded habit, though the larger size of the seeds ensured by the reduction in number may have had advantages in germination.

CONCLUSIONS

According to this interpretation of the remarkable petrified forest of the Cerro Cuadrado region, it is unique in a number of respects amongst other petrified forests. The abundant material of petrified and fertile seed cones of the two dominant types of tree gives a basis for a fairly satisfactory systematic comparison with other living and extinct conifers : the structure of the embryos, for example, and of the vascularization of the cone-scales and ligule in the araucarian cones, are characters which one can hope to demonstrate only very rarely in fossil conifers, and close comparison with living species is impracticable without them. Conclusive evidence of only two species, both based on seed cones, has been found in the forest—*Araucaria mirabilis* ; and *Pararaucaria patagonica*, whose affinities are probably with the Taxodiaceae. The detached portions of wood, branches and twigs most probably belonged to one or other of these species, though critical proof of relationship is lacking. The presence of the numerous petrified seedlings affords a unique demonstration of regeneration, probably of the araucarian species, in the forest. Both the dominant species are extinct, but one, *A. mirabilis*, probably disappeared in the course of evolution of section *Bunya* of the genus *Araucaria*, while the other,

Pararaucaria patagonica, left no descendants, the family of the Taxodiaceae having disappeared from South America without having played a prominent part in its floras so far as may be judged from the scanty fossil evidence. The characters of *Pararaucaria* in particular suggest an age not younger than Cretaceous for the forest : for no close taxonomic comparison with any living genus can be made.

My grateful acknowledgments are due to the Dixon Fund of the University of London for the provision of a grant towards the expenses of section cutting. I wish also to record my thanks to Mr. W. N. Edwards for his encouragement and help during the examination of the British Museum collections, and to the Director of the École Supérieure de Géologie appliquée in the University of Nancy, to Professor R. Florin, Professor T. G. Halle, Professor T. M. Harris and Professor J. Walton for facilities and help afforded in examining specimens in their care.

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Note for p. 122.

The pith structure in the *Pararaucaria* cones resembles quite closely that of the stem in the living *Taiwania cryptomerioides*. Doyle M. H. & Doyle, J. (1948, *Proc. R. Irish Acad.*, **52**, B : 26, text-fig. 5) have demonstrated that the pith structure in stems of Taxodiaceae may be used as a diagnostic character for the genera, though corresponding observations for cone axis anatomy are not available.]